ECONOMIC BOTANY

Devoted to Applied Botany and Plant Utilization

Vol. 12 JULY–SEPTEMBER, 1958 No. 3

Conference on Economic Botany ... David J. Rogers

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Caro-Red, a New Provitamin A Rich Palm Oil
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The Natural History of Jojoba (*Simmondsia chinensis*) and Its Cultural Aspects ... Howard Scott Gentry

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P. M. Dauchert[illegible] and T. A. Wa[illegible]

Isolation of Constituents of Ginseng (*Panax quinquefolium*)
[illegible] and W. M. Laurene

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Conference on Economic Botany

The New York Botanical Garden is sponsoring a conference on economic botany on August 12 and 13, 1958. The purpose of the sessions is to attempt to formulate the aims and goals which can be incorporated in this presently ill-defined field.

A current viewpoint is that economic botany should concern itself with basic botanical, phytochemical, and ethnological studies of plants known to be useful or those which may have potential uses so far undeveloped. Economic botany is, then, a composite of those sciences working specifically with plants of importance to man.

To be assured that this is an appropriate starting point, it is necessary to have ideas presented from every aspect of the field. Those who must sell a finished product are aware of present needs and future possibilities; those who carry out research programs are aware of the capabilities of the plants and the problems still confronting them. The teaching aspects come in for their important role in first stimulating students toward a career and then providing a satisfactory curriculum to this end. At present there is little communication between the people interested in these aspects.

We hope then to formulate plans for economic botany which will assist all those whose problems deal with plants of importance to man to bring order from present chaos.

Although the number of participants invited to attend is small, those chosen represent most of the important endeavors which impinge upon the field of economic botany. The conferees represent teaching, research, and commercial organizations, both public and private.

Many laboratories and experiment stations devote full time to experiments designed to increase yield, produce longer, resist better—a host of such important factors in plant utilization—but in few places may one find studies on the same plants at a purely botanical or phytochemical level. What are the botanical studies of importance? These are experiments primarily made for the botanical information inherent in them and not specifically based upon the desire for a specific answer to a utilization problem. They are studies of the variations of economic crops from the standpoint of their classification, and the basis of the variation in the genetic mechanisms which operate. Examination of the evolution of economic plants, which shed light primarily on one of the most intriguing biological problems, yield as by-products the possible prediction of new variation within a group. There are other fascinating and highly important problems in economic plants: the mechanisms by which plants produce certain significant products—oils, fats, waxes, gums, resins, latex, alkaloids, etc.—and the purposes which these serve in the plants.

We must also remember that the study of economic plants has uses other than purely commercial. Through the proper employment of ethnobotany, many problems of civilization, past, present, and future, can be elucidated.

It has been demonstrated that, on those occasions where basic studies have been made, there is real significance for later developmental stages in agriculture. One of the most striking examples which one might cite is the case of Shull's work on hybrid corn, where curiosity concerning the effects of breeding of pure lines

and the results of hybrids from these has been responsible for tremendous profits. Stapf's classification of the oil-grasses, done purely for the taxonomic importance, has led producers of essential oils to new and greater profits.

Our conferees do not have to have the value of these pointed out to them, for they are well aware of the significance of this type of research. It is our problem to stimulate more scientific interest in the field, for economic botany is of the most fundamental importance to man.

DAVID J. ROGERS

The Effects of Gibberellin on Economic Crops[1]

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INTRODUCTION

Gibberellin, the generic name of several closely related chemical substances of which gibberellic acid is the best known, exerts marked effects on plant behavior. Within the past three years plant physiologists and horticulturists of the western world have moved into exciting areas of research with these chemicals which had an oriental beginning over 32 years ago. Kurosawa (97) discovered that filtrates from the fungus *Gibberella fujikuroi* (Sawada) Wollenw. which caused the "Bakanae" or "foolish seedling disease" of rice—so named because infected plants grew unusually tall and then died—produced the same "overgrowth" stimulation as the disease. This suggested that the fungus produced a substance causing the Bakanae symptoms. Kurosawa and others attempted, but failed, to isolate the active principal. It remained for T. Yabuta and Y. Sumiki (Fig. 1) of the University of Tokyo to characterize gibberellin, and the discovery was announced in 1938 (202).

Not until 1955–56 did active research in the western hemisphere begin with these substances on economic crops. Since then a number of reviews of the history, physiological action, and agricultural potentialities of the gibberellins have appeared (9, 22, 23a, 59, 81, 120, 137, 137a, 161 175, 176, 190, 199, 204). Concurrent with these reviews producers of gibberellin have prepared several summaries and literature abstracts.[3]

Four gibberellins—A_1, A_2, A_3 (gibberellic acid), and A_4 (179)—have thus far been isolated from filtrates of the fungus, *Gibberella fujikuroi*. It is now well known that "gibberellin-like" substances are widely distributed in actively growing reproductive and vegetative tissues of higher plants (33, 103, 125, 127, 143, 154, 155, 158). Of significance is the recent isolation of gibberellin A_1 from *Phaseolus multiflorus* Lam. (130). The many unique plant responses that have been recorded following treatment with gibberellin and the rapidity with which greenhouse and field testing has proceeded in diverse areas of crop production suggested the need for an appraisal of agricultural utility which is the objective of this paper.

GENERAL EFFECTS OF GIBBERELLIN ON GROWING PLANTS

1. Practically all are affected and respond by more rapid growth and elongation if penetration is affected on parts actively growing or still capable of growth.

2. A given species or variety responds to a wide range of concentrations, and

[1] Journal Article No. 2262 from the Michigan Agricultural Experiment Station.

[2] The authors gratefully acknowledge the financial assistance of Merck and Co. and the Chas. Pfizer Co. in some of the original studies reported herein.

[3] "Gibrel", Merck and Co., Inc. Rahway, N. J.; "Abstracts of Current Research on the Effects of Gibberellic Acid on Plants", Bul. 512-3, Velsicol Chem. Corp., Chicago, Ill.; "Gibberellin Fact Book", Eli Lilly and Co., Indianapolis, Ind.; "Gibberellic Acid and Gibberellic Acid Bibliography", Plant Protection Ltd., Fernhurst Research Station, Surrey, England. Since this manuscript was submitted the "Source Book of Gibberellin", a monumental work prepared by Dr. Frank H. Stodola, has come to the authors' attention.

different species and varieties within a species react differently to the same treatment. Young plants are more sensitive than old, but as with environmental stimuli, a certain size has to be attained before flowering can be accelerated.

3. Amounts needed to produce noticeable effects are small, ranging from one-thousandth to several hundred micrograms per plant, or a fraction of a gram to several ounces per acre.

4. The most effective and efficient method of application is to the growing plant in water solution as a foliar spray, although seed treatments and "in the furrow" applications have proven useful on young seedlings.

5. Some effects on herbaceous plants are noticeable within hours, while a discernible response on woody plants may take several days or weeks.

6. Gibberellin is highly mobile and distribution is systemic in most herbaceous plants but not necessarily in woody plants or those with large storage tissues. Responses are often induced at points considerably removed from the site of application; accordingly, complete coverage in foliage applications may not be essential.

7. The stimulatory effects are temporary; thus, for a continuing response repeated dosages are necessary.

8. Both cell enlargement (elongation) and normal cell division are promoted. These properties are not unique, however, with gibberellin since they also reside in many naturally occurring substances extractable from plants and have a number of parallels among the synthetic auxins and kinins.

9. The primary stimulus is on growth of plant parts above ground. Leaf areas and length of the main stem axis are increased. Upright plants grow taller, and prone plants become more upright. Root

FIG. 1. The discoverers of gibberellin, Drs. T. Yabuta (left) and Y. Sumiki, University of Tokyo (Photograph courtesy of Dr. Y. Sumiki).

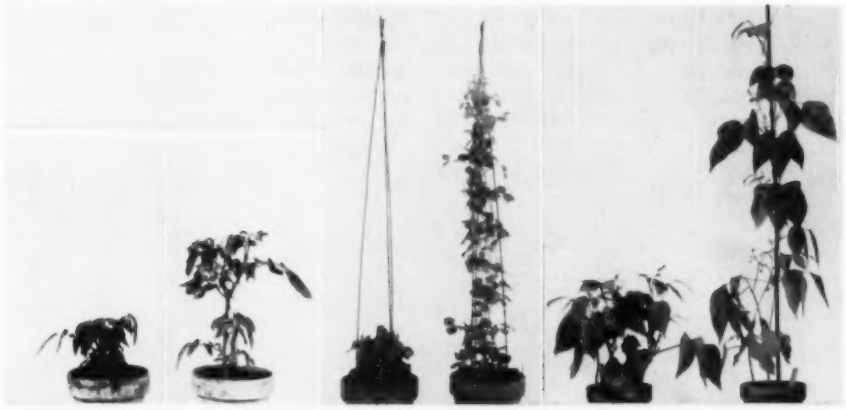


FIG. 2. The effects of gibberellin on the growth of dwarf plants. Left to right: a dwarf tomato, Progress peas, and Contender beans. Control plants on left, gibberellin treated on right.

growth and enlargement may be significantly altered under some conditions.

10. New growth is often paler green or chlorotic. This can be partially offset by maintaining high fertility levels, particularly nitrogen.

11. Crop response is often greatest when growth is retarded by subnormal temperatures, low light intensities, short days and deficient moisture.

12. Plant composition (concentration of organic and mineral constituents) is not appreciably altered, although one notable exception has been reported (149a).

GROWTH RESPONSES

Dwarf and Non-Dwarf Plants

The most dramatic differences in height following treatment with gibberellin (Fig. 2) have been observed with genetically dwarf mutants and highly determinant varieties of crop plants (3, 19, 21, 24, 56, 86, 153, 191). This has tended to

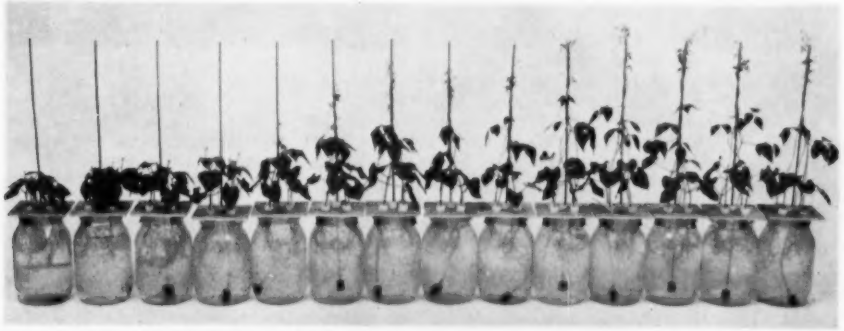


FIG. 3. Growth response of beans (var. Blue Lake) to various amounts of a mixture of gibberellin A_1 and A_3, 120 hours after treatment. After Bukovac and Wittwer (24).

Left to right:

μg plant	.00	.01	.02	.05	.10	.25	0.5	1	2	5	10	25	50	100
Height in cm.	7	9	11	13	16	21	28	31	35	43	43	43	42	42

divert attention from normal types and even prompted the suggestion that tall or pole type varieties respond but little if at all (19, 21, 23). That this may not always be so is revealed by Fig. 3 in marked effect occurs at short photoperiods (Fig. 4). While the reversal of genetic dwarfism and promotion of twining growth (124) with gibberellin is of considerable academic interest since it

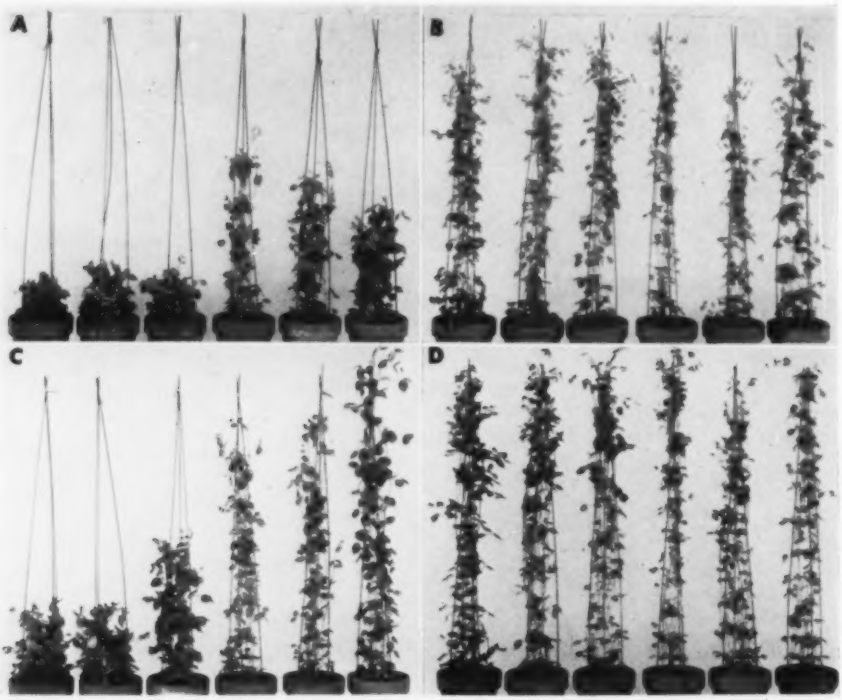


FIG. 4. Effects of gibberellin on the growth of dwarf, intermediate and tall pea varieties grown under short, 9 hr. (top), and long, 18 hr. (bottom), photoperiods. Left (A and C), controls—not treated; right (B and D) plants sprayed with 100 p.p.m. solution of gibberellin after first two leaves had unfolded. Varieties in A, B,C, and D from left to right, and in order of decreasing dwarfness when grown under long days without gibberellin as in C; Progress No. 9, Little Marvel, Early Perfection, Alaska, Thomas Laxton and Alderman. Note that tall varieties of peas (Alaska, Thomas Laxton and Alderman) show little or no differences in height when treated with gibberellin under long days (C and D), but a significant increase under short days (A and B).

which Blue Lake pole beans have been found highly sensitive as a bio-assay to extremely low dosages (0.01 μg./plant) and they also respond to a wide range of concentrations (24). Admittedly, tall pea varieties show little response to gibberellin if grown under long days, but a offers a biochemical basis for heritable characteristics, it is not likely that such findings will have agricultural utility. Yields and performance of treated dwarfs, though much higher than otherwise, seldom exceed the normal types (82). On the other hand, the reversal of

physiologic dwarfism (10, 147) in the apple (*Malus arnoldiana* Sarg.) and peach (*Prunus Persica* Batsch) could be useful in eliminating or reducing after-ripening procedures for the propagation of many tree fruits and ornamentals.

Leaf Expansion and Changes in Leaf and Shoot Morphology

An increase in leaf area and other photosynthetic surfaces has been suggested (22) as the probable explanation for increases in yield of up to 40% in crops such as celery and forage grasses following a single application of gibberellin. Numerous other plants (18, 24, 43, 65, 132, 132a, 152, 159, 177, 178) have shown dry weight increases of somewhat lesser magnitudes. The reports of Haber and Tolbert (67a) and Noggle (148) that gibberellin does not enhance the rate of CO_2 fixation per unit of leaf tissue support the increased leaf area hypothesis as the explanation for dry matter increases. Growth responses from gibberellin can also occur in the dark (78, 115, 180a). Gibberellin does promote overall leaf expansion and elongation with a wide variety of species, and a typical test with bean plants resulted in increases of 16 to 29 percent in the surfaces of primary leaves (Table I).

TABLE I

EFFECT OF GIBBERELLIN AND STAGE OF DEVELOPMENT UPON THE EXPANSION OF THE PRIMARY LEAF OF THE BLUE LAKE BEAN (*Phaseolus vulgaris* L.), 24 HOURS AFTER APPLYING 10 MICROGRAMS OF GIBBERELLIN

Percent expansion of primary leaf at time of treatment	Gibberellin	Leaf area	
		Square centimeters	Percent of control
20–30	–	12.4	...
	+	16.0	129
45–55	–	21.6	...
	+	26.1	121
75–85	–	25.6	...
	+	29.7	116

With celery (Fig. 5) and rhubarb, treatment was reflected by broader blades and longer petioles, and in the former the larger petioles have resulted in substantial yield increases (91, 149, 180, 197). Differences in leaf and shoot morphology as well as size and thickness have been the subject of other investigations (65, 70a, 92, 95, 96, 135, 159, 164, 165, 197), but it is not likely that all yield responses can be resolved by these variables.

Regrowth of fall spinach (*Spinacia oleracea* L.) after an initial cutting and during cool weather has been stimulated with gibberellin, and the leaves of treated plants are more upright and thus adapted for mechanical harvesting (137a, 200).

The tobacco plant (*Nicotiana Tabacum* L.) was the object of much early research by the Japanese (176), and it appears with this crop grown primarily for its leaves or leaf products that important and perhaps desirable changes in breadth, thickness, and composition (nicotine content) might be induced (49, 149a)

Vegetative Extension, Plant Heights, Dry Matter Accumulation and Crop Yields

The most apparent and widespread effect of gibberellin is a promotion of growth by stem elongation and an increase in height, not necessarily reflected by greater weight or volume. Hundreds of herbaceous and woody plants, ranging from orchids and succulents to evergreens, shade trees and forest crops have responded (2, 2a, 5, 9, 24, 39, 41, 55, 68, 73, 90a, 92, 98, 107, 132, 132a, 136, 145, 156, 157, 165, 190). In general, rapidly growing herbaceous plants require only low dosages of gibberellin and are particularly responsive if extra fertilizer, especially nitrogen, is provided (157).

Some of the earliest reports from the

western hemisphere (18, 24, 106, 140) emphasized that total dry weights were increased on many herbaceous plants treated with gibberellin. The highly transient nature and non-predictability of such increases have become all too apparent in recent years. Some crops, and even varieties within a crop, but not others, have shown increases (18, 24). Gains in dry weights of tops are often not accompanied by corresponding increases in root weights (3, 18, 24). Age of the plant when treated appears important as well as the number and frequency of applications (24, 141, 197). Temperature and particularly photoperiod exert a marked influence (Tables II, III and IV). Indeed, many of the contradictory results pertaining to dry matter increases following treatment with gibberellin might be resolved by a consideration of the photoperiod under which the experiments were conducted.

FIG. 5. Effects of gibberellin on the growth of Early Fortune (Golden Plume type) celery 19 days after treatment. Left, control (no treatment); right (row in background) 100 p.p.m., the equivalent of 15 grams per acre, of gibberellin applied as a foliar spray. Average petiole length of treated celery was 10 inches compared to 8 inches for the controls, and stalks were 40 percent heavier. Treated celery was also better blanched. Photographed at Thomas Bosgraaf and Sons Celery Farm, Hudsonville, Michigan. After Wittwer and Bukovac (197).

That gibberellin has no promotive ef-

TABLE II

EFFECTS OF GIBBERELLIN ON DRY WEIGHT ACCUMULATION IN TOPS AND ROOTS OF SEVERAL ECONOMIC CROPS GROWN AT THE PREVAILING LATE SPRING AND EARLY SUMMER PHOTOPERIOD (14–16 HRS.) AND AT 13–16° AND 18–21° C. IN CULTURE SOLUTIONS

Plant	13–16° C.				18–21° C.			
	Tops		Roots		Tops		Roots	
	−GB	+GB	−GB	+GB	−GB	+GB	−GB	+GB
	(Milligrams dry weight per plant)							
Celery (*Apium graveolens* L.[1])								
Cornell 19	302	320	65	45	489	619	65	59
Utah 10-B	379	443	67	76	527	704	78	88
Bean (*Phaseolus vulgaris* L.[2])								
Blue Lake	941	917	240	150	1159	1183	169	143
Contender	1341	1236	261	204	1641	1473	274	186
Michilite	266	278	61	52	428	351	73	51
Sanilac	307	293	77	57	433	389	80	55
Pea (*Pisum sativum* L.[2])								
Alderman	87	93	39	40	129	124	44	33
Little Marvel	89	124	40	38	132	171	51	43
Sweet corn (*Zea Mays* L.[1])								
Golden Cross	69	47	30	23	121	116	61	42
North Star	90	68	34	22	150	193	52	58

[1] Determined 20 days after treating.
[2] Determined 12 days after treating.

fect on initiation or growth of roots has been generally accepted, but exceptions to this concept have already appeared (48, 163). Whereas there is usually no effect of low concentrations of gibberellin on root growth, somewhat higher dosages definitely retard elongation of roots of several species of germinating

TABLE III

EFFECT OF GIBBERELLIN AND TIME OF APPLICATION ON FRESH WEIGHT AND PETIOLE LENGTH OF TWO VARIETIES OF FIELD GROWN *Apium graveolens*

Celery variety	No treatment (control)	Single application (days before harvest)				Repeat application (days before harvest)	
		26		16		26 and 16	
		10 p.p.m.	100 p.p.m.	10 p.p.m.	100 p.p.m.	10 p.p.m.	100 p.p.m.
		Fresh weight per plant (gm.)					
Cornell 19	386	377	454	459	450	413	377 *
Utah 10-B	422	522	509	459	454	527	522 *
		Length of 2nd outer petiole (cm.)					
Cornell 19	18.5	19.8	21.6	20.3	21.8	20.6	23.6
Utah 10-B	19.3	22.7	24.4	22.7	24.5	23.6	26.7

* Approximately 30% produced seedstalks.

TABLE IV

EFFECT OF GIBBERELLIN ON DRY WEIGHT ACCUMULATION OF *Pisum sativum* L. AND *Apium graveolens* L. GROWN AT A SHORT (9–11 HRS.) AND LONG (18 HRS.) PHOTOPERIOD

Plant and variety	Photoperiod and treatment			
	9–11 hours		18 hours	
	−GB	+GB	−GB	+GB
	(*grams per plant*)			
Pea (*Pisum sativum* L.)				
Greater Progress	.16	.32	.30	.49
Little Marvel	.17	.30	.36	.54
Early Perfection	.17	.23	.31	.40
Thomas Laxton	.16	.20	.26	.29
Alaska	.18	.18	.34	.36
Alderman	.24	.33	.41	.50
Celery (*Apium graveolens* var. *dulce*)				
Cornell 19	.41	.45	.48	.48
Utah 10-B	.49	.59	.77	.82

seedlings (Table V). Similarly, gibberellin antagonizes the rooting response induced by 3-indoleacetic acid and 2-naphthaleneacetic acid (21). An additional complication arises in that gibberellin may affect the absorption (171), transport (3, 8), and redistribution of materials from the shoot to root and root to shoot, and this effect for foliar absorbed phosphate is opposite to that induced by maleic hydrazide (Table VI).

A serious field hazard in the use of gibberellin for enhancing yields of vegetation or dry matter lies in the unfavorable balance temporarily created between top and root growth, and thus crops may be subject to undue moisture stress and temporary nutrient deficiences,

TABLE VI

EFFECT OF MALEIC HYDRAZIDE AND GIBBERELLIN UPON THE DISTRIBUTION OF FOLIAR ABSORBED P^{32} LABELED PHOSPHATE IN *Phaseolus vulgaris* L. (BLUE LAKE)

Maleic hydrazide (p.p.m.)	Stem P^{32}/Root P^{32}			
	Gibberellin (μg./plant)			Mean
	0	10	100	
0	7.6	15.7	19.1	14.1
100	5.8	18.7	15.2	13.2
500	3.2	4.0	8.5	5.2
1000	2.8	5.3	4.3	4.2
Mean	4.9	8.4	11.8	...

TABLE V

EFFECT OF VARIOUS CONCENTRATIONS OF GIBBERELLIN UPON ROOT ELONGATION OF GERMINATING SEEDLINGS OF SEVERAL PLANTS (10 ML. OF GIBBERELLIN SOLUTION PER PETRI DISH)

Plant	Gibberellin (p.p.m.)						
	0	10	100	500	1000	2500	5000
Cucumis sativus L. (cucumber) Wisconsin SR-6	5.7	5.0	4.5	3.0**	1.3**	0.3**	0.1**
Fagopyrum esculentum Moench. (buckwheat) var. Japanese	5.8	5.0*	4.1**	0.8**	0.0**	0.0**	0.0**
Pisum sativum L. (pea) Little Marvel	4.0	3.7	3.5	3.0*	1.9**	1.2**	0.4**
Zea mays L. var. *rugosa* Bonaf. (sweet corn) Golden Cross	6.7	5.4*	5.4*	4.0**	1.8**	0.5**	0.4**

* or ** Differs significantly from controls at the 5 and 1 percent levels, respectively.

with all accompanying disorders, when soil moisture and fertility levels are marginal. This has been noted repeatedly in the lighter green (chlorotic) foliage, and wilting and burning out of terminal growth and scorching of leaves of treated plants during hot weather (24, 27, 68, 106, 132, 132a, 135, 140, 141, 157, 190, 194, 197, 198, 200).

spring and extended by several weeks in autumn (80, 106, 140, 141, 194). Mid-winter growth in cool weather has been induced in an otherwise winter-dormant Brazilian pasture grass, *Panicum maximum* Jacq. (61). Growth which would not have occurred because of low temperatures has been induced on *Camellia japonica* L. (116) and young grapefruit

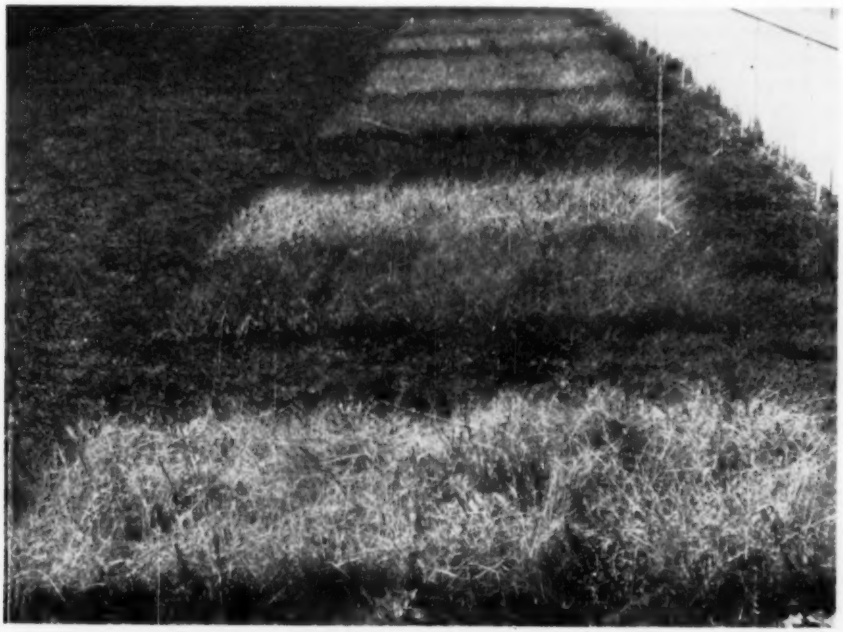


FIG. 6. The effect of gibberellin in promoting the growth of grass (predominantly *Poa pratensis*, var. Kentucky bluegrass) in early spring. Rectangular plots (15 square feet each) starting in the foreground and going toward the back were sprayed March 5, 1957, with aqueous solutions containing 1,000, 0, 100, 1,000, 10, 0, 100, 0, 1,000, 100, 10, 1,000, 0, 100, and 10 p.p.m., respectively, of gibberellin. Photographed April 1, 1957. After Wittwer and Bukovac (194).

Promotion of Growth at Subnormal Temperatures

A notable effect of gibberellin on an unusually large number of plants is that the temperature optima for growth appear to be broadened and the minima lowered. Growth of forage grasses is initiated (Fig. 6) much earlier in the

trees (*Citrus paradisi* Macf.) (44). Coleman (43) reports that the most pronounced effects of gibberellin on the growth of sugarcane (*Saccharum officinarum* L.) occurred when environmental conditions were unfavorable for normal vegetative growth, specifically during drought periods in the summer and the extremely cold conditions of November,

1957, when under field conditions heights of treated plants in the latter instance were increased 300% above the controls. The possible use of gibberellin in promoting rapid flower development of *Cyclamen indicum* Auth. during adverse summer environments has also been suggested (93).

Gibberellin seed treatments (Fig. 7) have promoted earlier, more uniform emergence, and a better stand with a variety of crops (7, 14, 82, 84, 86, 139, 196), although there are many reported failures (13, 53, 57, 90a, 152, 152a, 168, 170) and in some tests, seedlings were decotyledonized and hypocotyls split during emergence (57, 149, 196). The promotive effects of gibberellin seed treatments on seedling emergence have been most apparent in early spring when temperatures were otherwise too low for normal performance. More rapid emergence under such conditions should enable farmers to begin weed control earlier and reduce hazards from insects and diseases that affect germinating seedlings. The heat-sum requirements for emergence of peas and beans have been reduced 20 to 30%. Slurry seed treatments of gibberellin for peas and beans (including soybeans) also have promise for producing taller plants with longer stems more adaptable to direct combining or mechanical harvesting (3b, 149, 196).

The concept that gibberellin responses are most pronounced when climatic limitations for growth are greatest is now based on a considerable body of evidence (42, 43, 61, 80, 84, 106, 114, 140, 141, 194, 201). This unique, and until now almost ignored, effect of gibberellin in partially overcoming the growth restricting effects of temperature, light, and moisture should serve as a challenge to horticulturists and agronomists to apply this important control of plant behavior in numerous areas of crop production; and to the plant physiologist and biochemist the resolution of the action by which gibberellin modifies climatic control of growth should be a fruitful area of research.

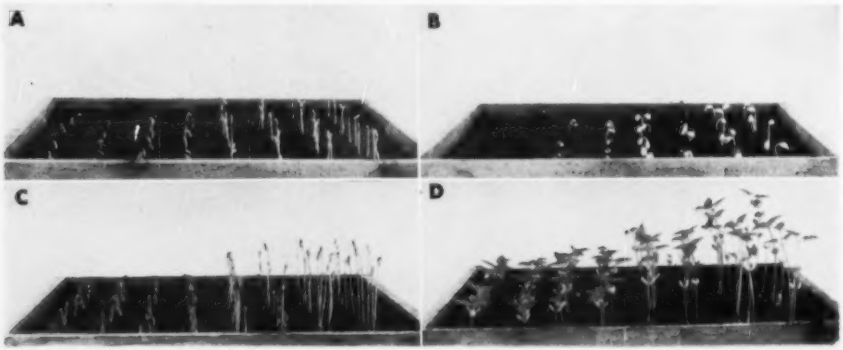


FIG. 7. Effects of gibberellin in slurry seed treatments on emergence of Alaska peas (A and C) and Sanilac beans (B and D), at 13° (A and B) and 18° C. (C and D). Paired rows in either A, B, C or D, left to right: treated with seed protectant slurry (Delsan AD) only, seed protectant slurry + 500, + 2500, and + 10,000 p.p.m. of gibberellin.

FLOWERING RESPONSES

Biennials

The discovery that stem elongation and flowering in *Hyoscyamus niger* L. (100) could be induced with gibberellin was at first a minor sensation. It was

soon apparent, however, that gibberellin was effective only under long days and that other cold-requiring biennials, with a few exceptions, did not respond so favorably. Among the many biennials which have specific cold plus long-day requirements for flowering, there are no examples in which both the temperature and photoperiod requirements for flowering can be replaced with gibberellin. Biennials which have flowered irrespective of daylength have done so reluctantly and have either a facultative or no long-day requirement (Tables VII, XVII). Furthermore, with the possible exceptions of certain varieties of *Daucus carota* L. (25, 50), *Digitalis purpurea* L. (15, 111), and *Matthiola incana* R. Br. (113), gibberellin effectively accelerates flowering in cold-requiring biennials only when (a) the photoperiodic requirement for flowering is satisfied, (b) they are maintained at temperatures slightly above those inductive for flower formation, (c) they are treated after the cold requirement is partially satisfied or (d) the biennial characteristic is weak (25, 37, 62, 63, 100, 102, 111, 134, 169, 177, 189, 190, 192).

TABLE VII

COLD-REQUIRING BIENNIALS IN WHICH FLOWERING HAS BEEN ACCELERATED BY GIBBERELLIN. AFTER WITTWER AND BUKOVAC (192)

Plant	Treatments
Apium graveolens L. var. *dulce* Pers. (celery) Cornell 19 and Utah 10-B	1 foliage spray of 1000 p.p.m. at 12–15 leaf stage
Beta vulgaris L. (sugar beets) U.S. 400	4 foliar sprays of 1000 p.p.m. at 3–4 wk. intervals
Brassica oleracea L. var. *capitata* (cabbage) Golden Acre and Ferry's Round Dutch	100 μg. or foliar sprays of 1000 p.p.m. weekly for 8 wks. First treatment at stem diameter of 1 cm. and 7–9 leaves
Brassica oleracea L. var. *acephala* DC. (kale) Siberian and Dwarf blue curled	(As above for cabbage)
Brassica oleracea L. var. *acephala* DC. (collards) Georgia and Louisiana Sweet	100 μg. weekly or foliar sprays of 1000 p.p.m. for 6 wks. at 7–9 leaf stage and 1 cm. stem diameter
Brassica Napobrassica Mill. (rutabaga) Purple Top	3 foliage sprays of 1000 p.p.m. at 2-wk. intervals at the 6–9 leaf stage
Brassica Rapa L. (turnip) Purple Top	(As above for rutabaga)
Daucus Carota L. var. *sativa* DC. (carrots) Chatenay and Imperator	20–100 μg./plant when roots were 1 cm. or larger in diameter
Digitalis purpurea L. (foxglove)	100 μg./plant for 6 wks. at the 6–8 leaf stage or 1000 p.p.m foliage spray
Bellis perennis L. (English Daisy)	(As above for foxglove)
Matthiola incana R. Br. (stock)	20–100 μg./plant at the 6–8 leaf stage or a foliage spray of 100 p.p.m.
Viola tricolor L. (pansy)	(As above for stock)

Many cold-requiring biennials are also obligate long-day plants, and while gibberellin will completely or, more often, partially replace the temperature requirement, it is unable to substitute for the photoperiodic requirement (37, 100, 169). With truly biennial sugar beet varieties having a specific cold-requirement for flowering, gibberellin has little effect on flowering unless (a) the plants are simultaneously or subsequently grown in long days, (b) temperatures are maintained within 2 to 3° C. of those normally inductive, and (c) repeated doses of gibberellin are applied (Fig. 8). Extensive stem elongation also precedes flower formation. Most cold-requiring biennials of economic importance (192) as well as wild species of *Phacelia* (64) follow the pattern of the sugar beet in response to gibberellin.

Though the limits of effectiveness of gibberellin in accelerating flowering are narrow for most biennial crops, and instances of poor seed-set have been reported (50, 102), its utilization in com-

mercial greenhouse flower production, in speeding up variety improvement programs, in roguing of plants susceptible to bolting, and in seed production can be envisaged (Fig. 9). There is no evidence of a gibberellin effect transmitted by seeds harvested from a gibberellin-treated plant. Such seeds have been viable and produced normal seedlings (25, 50, 62, 190, 193).

FIG. 8. Effects of gibberellin on the flowering of sugar beets (var. U.S. 400) grown under a 9-hour (A and B) and an 18-hour (C and D) photoperiod. Plants maintained at a night temperature of 13° C. which was close to that inductive for flowering if combined with long days. Growing tips of plants in B and D sprayed 4 times at 4-week intervals with 1000 p.p.m. solution of gibberellin. A and C consisted of controls at 9- and 18-hour photoperiods, respectively. Seed planted September 17, 1957, and plants photographed January 24, 1958. Order of flowering was D, C and B, with D flowering 30 days in advance of C, and C flowering approximately 60 days in advance of B. No flowering occurred in A, and extensive stem elongation preceded flowering in both B and D. After Snyder and Wittwer (169).

Long-Day Plants

The report of gibberellin-induced flowering in the biennial, *Hyoscyamus niger*, was followed closely by equally significant communications on long-day plants, the first by Bünsow and Harder (30). Gibberellin applied to plants grown in short photoperiods accelerated flowering in those having a facultative long-day requirement and induced flowering in many having obligate long-day requirements (27, 31, 32, 71, 101, 102, 104, 109, 111, 118, 119, 123, 127, 192, 193, 198). Several winter annuals have been included among the long-day plants responding by earlier flowering to gibberellin (27, 71, 104, 193, 198). Other winter annuals have shown no response (102, 122).

With many facultative long-day plants gibberellin significantly accelerates flowering and stem elongation not only when they are grown in short but also under long days (Table VIII). The most pronounced differences were, however,

TABLE VIII

MODIFYING EFFECTS OF FOLIAR SPRAYS OF GIBBERELLIN ON THE PHOTOPERIODIC RESPONSES OF SEVERAL FACULTATIVE LONG-DAY PLANTS. AFTER WITTWER AND BUKOVAC (198)

Plant	9-hour-photoperiod			18-hour photoperiod		
	Gibberellin (p.p.m.)			Gibberellin (p.p.m.)		
	0	100	1000	0	100	1000
	(Days from seeding to appearance of visible flower buds)					
Raphanus sativus L. (radish) Comet	70	...	60 *	55	...	47 *
Centaurea Cyanus L. (centaurea) Cyanus Double	86	69 *	68 *	55	54	52
Brassica pekinensis Rupr. (Chinese cabbage) Michihli	110	104	87	88	81 *	75
Brassica juncea Coss. (mustard) Tendergreen *	116	95 *	80 *	92	84 *	80 *

* Flowering in significantly fewer days than controls ($P < 0.05$).

under the short photoperiod. The acceleration of flowering under both daylengths was generally proportional to the amount (concentration) of gibberellin and the frequency of its application. With Great Lakes head lettuce, a facultative long-day winter annual, the effects of gibberellin on flowering were more pronounced than those of temperature, photoperiod or seed vernalization (Fig. 10). All gibberellin-treated plants flowered (with a single exception) irrespective of the environmental conditions imposed (27).

TABLE IX

MODIFYING EFFECTS OF FOLIAR SPRAYS OF GIBBERELLIN ON THE PHOTOPERIODIC RESPONSES OF SEVERAL OBLIGATE LONG-DAY PLANTS. AFTER WITTWER AND BUKOVAC (198)

Plant	9-hour photoperiod			18-hour photoperiod		
	Gibberellin (p.p.m.)			Gibberellin (p.p.m.)		
	0	100	1000	0	100	1000
	(Days from seeding to appearance of visible flower buds)					
Spinacia oleracea L. (spinach) Bloomsdale	No flowering	...	93	76	...	75
Cichorium Endivia L. (endive) Batavian	No flowering	117	112	102	95 *	94 *
Chrysanthemum coccineum Willd. Pyrethrum	No flowering	214	137	...	...	...
Chrysanthemum Parthenium Pers. Feverfew	No flowering	No flowering	No flowering	82	78 *	77 *

* Flowering in significantly fewer days than controls ($P < 0.05$).

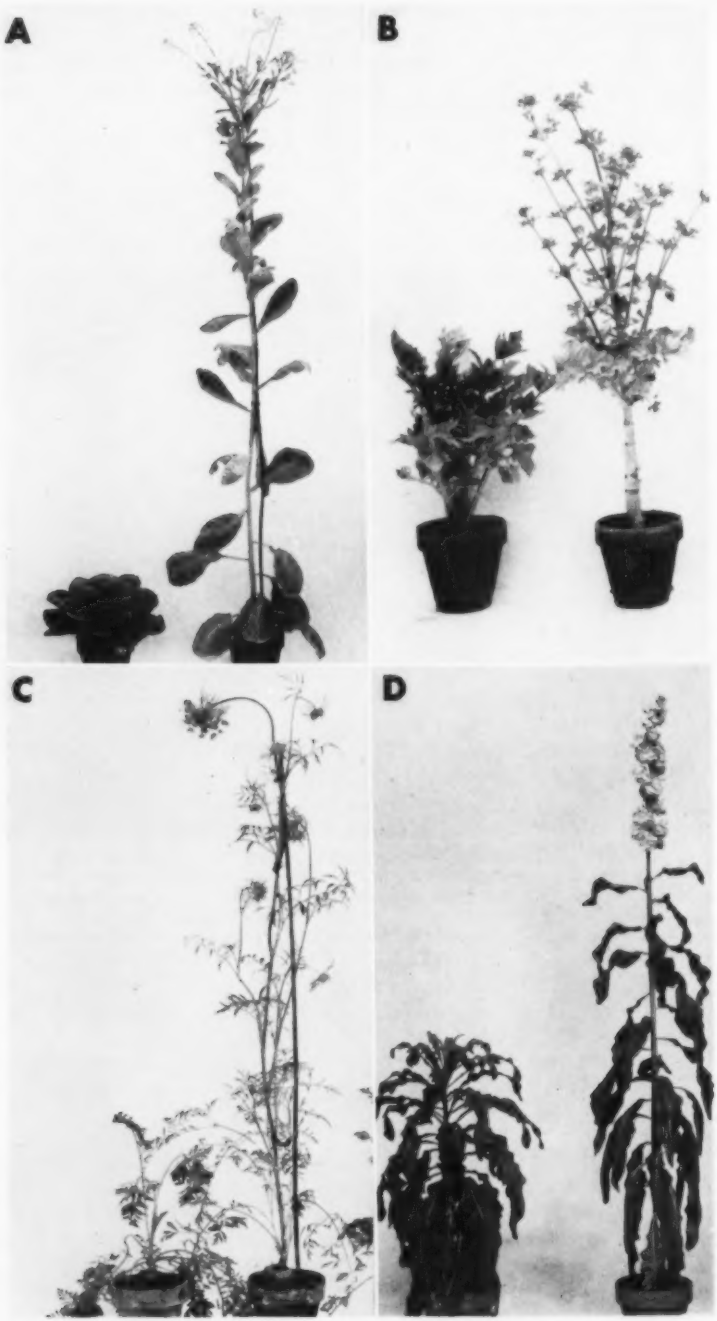

A
B
C
D

TABLE X

EFFECT OF GIBBERELLIN ON FLOWERING OF EIGHT *Lycopersicon esculentum* MILL. VARIETIES DIFFERING IN VEGETATIVE VIGOR AND FLOWERING HABIT. AFTER BUKOVAC, WITTWER AND TEUBNER (26)

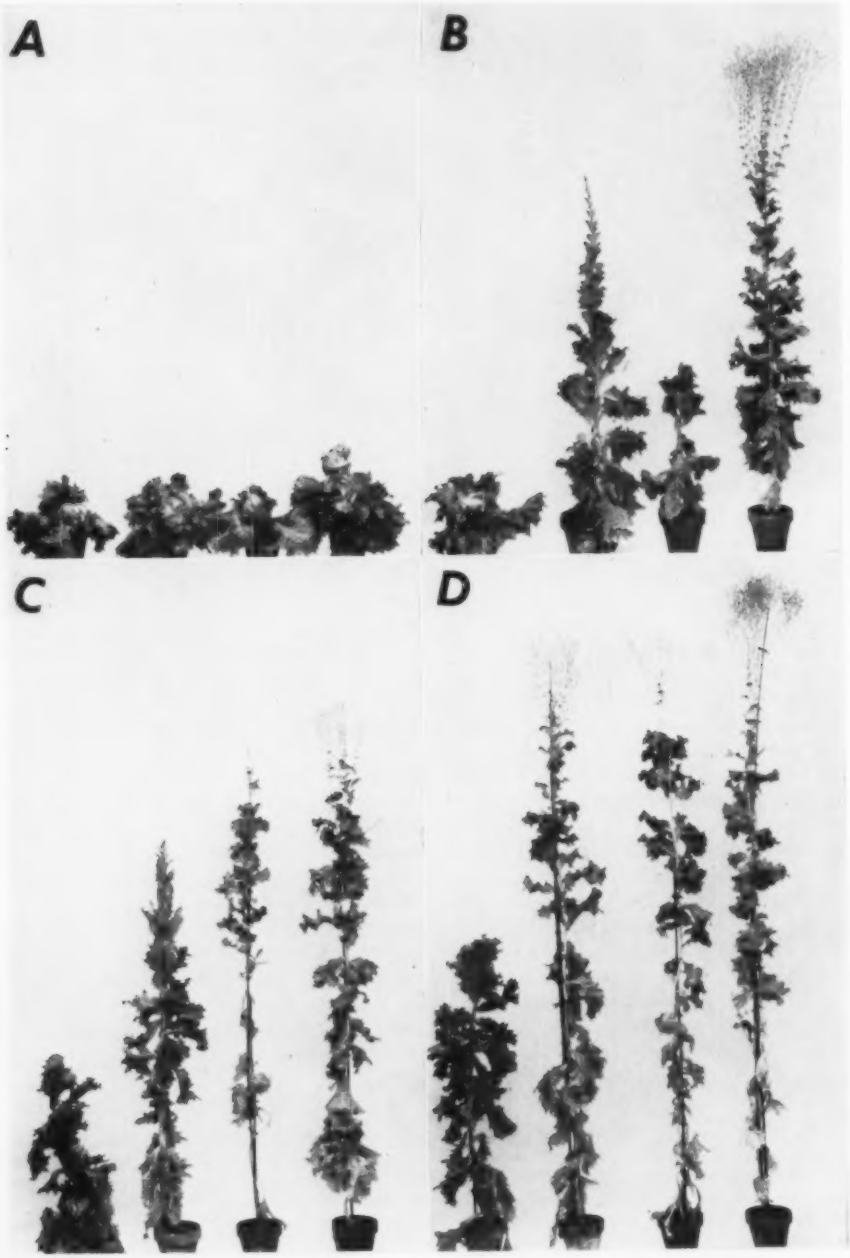
Tomato variety	Days to first anthesis		Nodes to first cluster		Flowers in first cluster	
	−GB	+GB	−GB	+GB	−GB	+GB
	(Means of 12 single plant replicates)					
Tiny Tim	41.9	39.8	5.3	7.7 **	10.1	6.1 **
Fireball	45.5	44.7	6.3	7.3 **	8.5	5.0 *
Dixville	46.4	45.9	6.9	8.2 *	19.8	7.4 **
Puck	47.8	46.3 *	6.8	9.8 **	7.3	8.5
Michigan-Ohio Hybrid	48.8	48.6	6.3	8.5 **	9.0	6.4 **
Moreton Hybrid	48.9	46.3 **	7.0	7.5 *	7.1	6.0
Dwarf Champion	50.3	46.9 **	7.7	9.5 **	5.3	4.8
Rutgers	51.3	50.3	7.3	9.3 **	7.8	5.8 *
Means	47.6	46.1 †	6.7	8.5 †	9.5	6.3 †

* or ** Differences between treated and control means of individual varieties significant at 5 or 1 percent levels, respectively.

† Differences between treated and control means of all varieties significant at the 1 percent level.

Stem elongation, but not always flowering, in obligate long-day plants grown under short days can be induced by gibberellin. Some effect on both stem elongation and flowering has, however, been detected under long photoperiods (Table IX). Gibberellin-induced flowering in the absence of prior stem elongation has been observed (198) as an exception to the rule that extensive stem elongation always precedes gibberellin-induced flowering in biennials, winter annuals and long-day plants grown under non-inductive environments. From reports thus far, it appears that gibberellin accelerates flowering and promotes stem elongation (the rosette is broken) in most all facultative long-day plants (192) and in some long-day–short-day plants (30), but the breaking of the rosette in many obligate long-day plants may not be followed by flowering (118, 119, 123, 169, 198). Stem elongation in some obligate long-day species continues only so long as gibberellin is regularly applied. When discontinued, secondary and tertiary aerial rosettes appear. It is of special significance that flowering has been induced in both biennials and long-day annuals by not only the gibberellins from *Gibberella fujikuroi*, but by extracts, containing substances similar to gibberellin from developing flowers or seeds of at least three widely different species of higher plants (33, 103, 125). As with gibberellin-induced flower formation in biennials, important agricultural uses may develop in the utilization of controlled flowering of long-day plants grown during winter in greenhouses in the north (109, 111, 113, 190), and in eccelerating flowering and maturity of seed crops in the west (72).

FIG. 9 (Opposite). Effects of weekly applications of gibberellin on stem elongation of several biennials; A—Ferry's Round Dutch cabbage, B—Cornell 19 celery, C—Chantenay carrots, and D—Lilac Lavender Stocks. Control plants on left, gibberellin treated on right. Gibberellin accelerates flowering in cabbage and celery if grown at temperatures close to those inductive for flowering, while in some varieties of carrots and stocks flowering may be induced several months in advance and over a wide range of temperatures.


A
B
C
D

Short-Day Plants

Flowering in several plants having an obligate short-day requirement grown under long days has not been induced with gibberellin (101, 102, 118, 198). Some acceleration of flowering has been recorded (198) for *Cosmos bipinnatus* Cav., a facultative short-day plant grown under long days, but most *Cosmos* plants in such tests eventually flowered if maintained indefinitely under a long photoperiod. No other instance of gibberellin-accelerated flowering of short-day plants grown in long days has been observed.

The flowering response, however, of several short-day plants grown under short days has been increased. With varieties of *Chrysanthemum morifolium* Ramat. differing in short-day requirement, applications of gibberellin during the third to seventh week of short days accelerated flowering by 3 to 12 days (35, 36, 110, 178). Measurements of size and stage of development of staminate inflorescences at specified times following short-day induction in *Xanthium pensylvanicum* Wallr. have shown an increase in flowering response (108). Similarly gibberellin can substitute for additional photoinductive cycles in promoting reproductive development of *Xanthium* plants induced to flower by a single long night and subsequently grown under long days (66). Quite by contrast, gibberellin greatly retarded but did not completely inhibit flowering of *Kalanchoë Blossfeldiana* v. Poellnitz. induced to flower by exposure to short days (69, 70, 70a). The effects of gibberellin on flower formation in many other facultative and obligate short-day plants, as well as short-day–long-day species grown under inductive short days and non-inductive long days have by no means been resolved and interesting relationships will yet be established.

Day-Neutral Plants

Flowering has been accelerated in some species and retarded in others having no specific day-length requirement (26, 132, 132a, 159, 190, 197), and not always are flowering responses clearly defined. In a detailed study of 20 tomato varieties differing greatly in vegetative growth and flowering behavior (26), treatment with gibberellin resulted in a consistent increase in node numbers preceding the first inflorescences

TABLE XI

EFFECT OF GIBBERELLIN ON THE COMPOSITION OF GEN LEVELS ON THE NUMBER OF STAMINATE FLOWERS PRECEDING THE FIRST PISTILLATE FLOWER IN *Cucumis sativus* L. (BURPEE HYBRID AND SMR-12)

Treatment	Control	Gibberellin
9-hour photoperiod		
Burpee Hybrid (slicing type cucumber)		
Low nitrogen	21.3 *	23.8
High nitrogen	14.0	47.8
SMR-12 (pickling type)		
Low nitrogen	5.3	7.3
High nitrogen	4.8	7.5
18-hour photoperiod		
Burpee Hybrid		
Low nitrogen	22.0	22.7
High nitrogen	19.0	32.8
SMR-12		
Low nitrogen	10.0	15.7
High nitrogen	6.2	15.7

* Least differences necessary for significance between any two values at the 5 and 1 percent levels are 12.4 and 16.8, respectively.

FIG. 10 (Opposite). Flowering and seekstalk development in Great Lakes lettuce plants as influenced by gibberellin, seed vernalization, temperature and photoperiod. A—controls, not vernalized and no gibberellin; B—vernalized and no gibberellin; C—not vernalized plus gibberellin; D—seed vernalized plus gibberellin.

Plants within each (A, B, C, D) group from left to right were grown as follows: 10–13° C. and 9-hour photoperiod; 10–13° C. and 18-hour photoperiod; 18–21° C. and 9-hour photoperiod; 18–21° C. and 18-hour photoperiod. After Bukovac and Wittwer (27).

and a decrease in flower numbers (Table X). Growth, however, was so accelerated that as a result the treated plants actually flowered earlier as measured by days from seeding. The acceleration of early growth and flowering may conceivably be utilized in the commercial production of early outdoor tomato varieties having determinate growth habits (Figs. 1 and 15).

FIG. 11. The effects of gibberellin on flower development and lasting quality of Spartan White geranium. Left, control (not treated); right, a foliar spray of 10 p.p.m. of gibberellin applied when the buds first began to open and showed color. After Lindstrom and Wittwer (112).

Monoecious Plants

The flowering behavior of both slicing and pickling types of *Cucumis sativus* L. and of *Zea Mays* L. following treatment with gibberellin has been observed. Gibberellin consistently increased the number of staminate flowers preceding the first pistillate flower in cucumbers (Table XI). The effects parallel those of long days and low nitrogen levels in the root media. Chemical regulation of this type of flowering, and of subsequent fruiting behavior first noted by the Japanese (203), is currently being studied for expediting mechanical harvesting of pickling-type cucumbers where crown set is not desirable. By contrast, in both sweet corn (*Z. Mays rugosa* Bonaf.) and inbred lines of field corn (*Z. Mays indentata* Bailey), sprays of gibberellin applied at critical stages of

plant development have suppressed microgametogensis and resulted in partially or completely sterile tassels (144, 197). The commercial possibilities for gibberellin-induced male sterility in inbred strains of corn used in hybridization await further study.

Other Effects on Flowering

More flowers, earlier flowers and larger flowers have been reported on a wide variety of potted and greenhouse-grown species (48, 93, 109, 110, 111, 112, 135, 156, 157, 165, 178). Truly remarkable increases in flower size (Fig. 11) occur with geranium (*Pelargonium hortorum* Bailey (48, 110, 112)) and hydrangea (*H. macrophylla* Ser., *H. arborescens* L., *grandiflora* Rehd. (135, 178)), and out of season production is a possibility with *Cyclamen indicum* (93).

Promotion of greater uniformity in flower-opening with the coffee tree (*Coffea arabica* L.) appears a reality (3a) which in turn should greatly reduce labor costs for harvesting and result in a product of uniform maturity and of high quality. Uniform opening of flowers in coffee may also be induced by exposure to low temperatures (188), but this is not feasible in the tropics. The results with coffee in the tropics suggest that similar research should be conducted with blueberries (*Vaccinium corymbosum* L.), red cherries (*Prunus cerasus* L.) and perhaps other fruits in temperate climates where uneven flowering results in a spread of maturity that increases the cost of harvest and lowers the quality of the product.

FRUIT SETTING AND FRUIT DEVELOPMENT

Tomato. Promotion of fruit-setting and of growth in the absence of pollination with gibberellin was first reported by Wittwer et al. (191) for the tomato. In the meantime, studies on fruit-setting and fruit-development of the tomato have been extended to many varieties and under diverse environments with essentially similar results (81, 85, 114, 151, 159, 190): (a) gibberellin is effective over a wider range of concentrations than any other known growth substance, (b) final fruit size and general appearance are inferior to that resulting from normal pollination or from many of the auxin-type chemicals (Table XII), unless gibberellin is used as a supplement to normal pollination or combined with other growth substances such as 4-chlorophenoxyacetic acid, and (c) there is no stimulatory effect from direct applications to the growing fruit. Results similar to those for the tomato have been observed on cucumbers, eggplant (*Solanum Melongena* L.) and peppers (*Capsicum frutescens* L.).

Application of gibberellin during flower development of greenhouse-grown tomatoes frequently resulted in abnormally elongated styles that extended beyond the stamen cone. Marked elongation of pedicles and peduncles and enlargement of sepals have also been common (200). Similar results have been observed for tobacco (49).

TABLE XII

RELATIVE EFFECTIVENESS OF *p*-CHLOROPHENOXYACETIC ACID, GIBBERELLIN A_3 AND 3-INDOLEACETIC ACID ON THE STIMULATION OF PARTHENOCARPY IN *Lycopersicon esculentum* MILL. (MICHIGAN-OHIO HYBRID) (FRUIT DIAMETERS 6 DAYS AFTER TREATING)

Compound	Molar concentration		
	3×10^{-5}	3×10^{-4}	3×10^{-3}
	(*Percent of non-pollinated control*)		
p-Chlorophenoxyacetic acid	117	228	231
Gibberellin A_3	141	159	166
3-Indoleacetic acid	110	155	207
Pollinated control	172		

Grapes. Some of the most dramatic and immediately useful effects of gibberellin in crop production may be with seedless type (*Vitis vinifera* L.) grapes of the Thompson Seedless and Black Corinth varieties. Two California research groups, one at the State Agricultural Experiment Station in Davis directed by Weaver (184, 185, 186, 187), the other at the Los Angeles Arboretum under Stewart (172, 173, 174), have reported that gibberellin sprays, of a wide range in concentration, applied at bloom or shortly thereafter result in greatly increased berry set and size and promote the formation of looser clusters. Results with gibberellin on seedless grapes have exceeded all expectations in that excellent sets of berries much larger than those from girdled vines or from spraying the flower clusters with 4-chlorophenoxyacetic acid have been achieved; and this has been coupled with no loss of quality and with pedicels 1½ to 2 times as long, thus resulting in no undesirable cluster compactness regardless of increased berry size. Proper timing of appropriate spray-dosages enables a realization of all favorable responses (Fig. 12). The practical advantages envisaged for the use of gibberellin on seedless grapes include the (a) increased

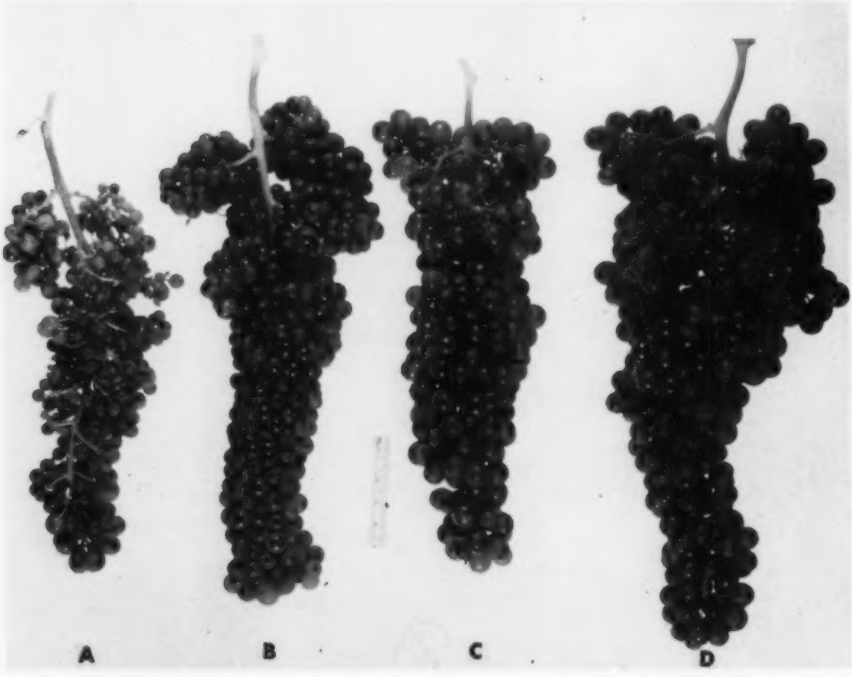


FIG. 12. Black Corinth grapes 59 days after being sprayed on May 31 gibberellic acid at 5 (C) or 20 p.p.m. (D). Control, A, and girdled but unsprayed, B. Berries sprayed with regulator at 5 p.p.m. are larger than girdled but unsprayed berries, but those sprayed at 20 p.p.m. are largest. Photographed July 30, 1957. (Photograph and legend, courtesy Dr. R. J. Weaver, University of California at Davis).

tonnage per acre resulting from increased set and size of clusters and berries (b) appreciable savings in girdling and cluster-thinning expenses, and (c) looser clusters facilitating better pest-control, making possible a higher quality fruit.

Though seeded berries respond much less to gibberellin than seedless varieties, some favorable effects have been noted in California (186, 187), and limited observations (105) suggest that gibberellin may also prove useful on eastern grapes (*Vitis labrusca* L.). Prebloom sprays tend to elongate the cluster parts. A high concentration (1000 p.p.m.) at full bloom is an effective thinning agent. Flowering has been hastened in some varieties. Spraying at full bloom and at berry set has resulted in greater fruit set, longer berries, advanced coloration, higher total solids, and looser clusters (187).

Deciduous Fruits and Citrus

Bartlett Pears (*Pyrus communis* L.). Attractive increases in fruit-set in Oregon have been reported (16) for Bartlett pears sprayed at full bloom with greatly varying concentrations of gibberellin, and these differences persisted till the crop was harvested. Harvested fruits were of normal size, but those from gibberellin-sprayed trees developed a fleshy protuberance at the calyx end. The abnormality, however, was not objectionable.

Calimyrna Figs (*Ficus carica* L.). Gibberellin has induced 95 to 100% parthenocarpic fruit-set and development and fruits matured a week earlier (45). As with tomatoes, seedless grapes, and Bartlett pears a wide range of concentrations proved effective when the chemical was applied at the time that pollination (caprification) and fruit setting normally occurred. If low (below 25 p.p.m.) concentrations of gibberellin prove effective for inducing parthenocarpy, and they very well could, without breaking the rest period of terminal buds, gibberellin may be of considerable benefit to the Calimyrna fig industry.

Apricot (*Prunus Armeniaca* L.). A temporary but markedly stimulated growth in fruit diameter of apricots has been reported following a single application of gibberellin at the beginning of pit hardening (46). The accelerated fruit growth rate was, however, followed by a period of depressed growth with the final result that the fruit matured a week later and with no effect on final size. It would be of interest to observe the effects of repeated applications on maturity and final fruit size.

Citrus. Significant increases in fruit set of limes (*Citrus aurentifolia* Swingle), lemons (*Citrus Limon* Burm.), Clementine mandarin (*Citrus deliciósa* Swingle) and navel oranges (*Citrus sinensis* Osbeck) have resulted from spraying the flowers or small fruit with 250 to 1000 p.p.m. of gibberellin (77, 169a). These increases were associated with no loss in final fruit size, nutritional or edible quality or color. Maturity was not affected. Fruit resulting from gibberellin-treated flowers produced navel oranges having slightly better color, thinner rinds, and a higher percentage of abortive seeds. Gibberellin applied to nearly mature navel oranges reduced rind thickness and coloration and increased juice content and the vitamin C concentration in the juice (40a). All such modifications of fruit quality noted on navel oranges would be notably beneficial for lemons.

Cotton. A striking effect in cotton (*Gossypium hirsutum* L.) boll retention studies has been reported from California (181, 182). The application of 0.25 ml. of a 1 to 100 p.p.m. solution of gibberellin to flowers in anthesis or to one- and two-day-old bolls negated or reduced flower abscission and boll shedding. Gibberellin also broke "cut-out" dormancy and prevented plants from

going into cut-out. (Cut-out dormancy in cotton is a cessation of vegetative and fruiting bud development apparently caused by the load of developing fruit preventing further fruiting and vegetative growth until some of the fruit-load matures or is removed). Weights of the additional bolls set by gibberellin were less, but fiber length was greater. The application of gibberellin to the entire plant, in contrast to direct treatment of flowers in anthesis or the young bolls, has not significantly increased yields or altered fiber and seed properties (6, 58, 83, 182).

Other Crops

Preliminary and very limited tests (1) with the Lambert cherry (*Prunus avium* L.) sprayed 22 days before harvest with 10 or 100 p.p.m. of gibberellin showed the fruit to be much more resistant to cracking.

Fruit setting has not been enhanced in the strawberry (*Fragaria* spp. L.), although a marked increase in elongation of inflorescences, petioles, peduncles and crown has been observed (167).

Chandler (38) suggests that gibberellin through its promotion of pollen tube growth, in some species, may be useful in stimulating fruit set and seed production where certain types of incompatibilities related to tube growth prevent fertilization before flower abscission.

DORMANCY

Potato Tubers. Dormancy in new or "green" potato (*Solanum tuberosum* L.) tubers may be shortened appreciably by treating with gibberellin. Recent field observations (129) suggest a one- to two-minute dip in a solution containing 1.0 p.p.m. of gibberellin for dormant or semi-dormant seed pieces, while somewhat weaker solutions (0.5 to 0.25 p.p.m.) are effective on old seed. These concentrations are considerably below those used in some of the initial studies with gibberellin for breaking dormancy and inducing sprout growth in potatoes (113a, 160, 161, 162). Earlier and more uniform sprouting with hastening of crop maturity has resulted from treatment of non-dormant as well as dormant tubers. Promotion of uniform sprouting (Fig. 13) and earlier emergence could become important objectives for using gibberellin in commercial potato production. "Lateral buds" on gibberellin-treated seed pieces from the basal portions of the tubers grow as rapidly as the "terminal buds" on the apical end. Needed quantities of gibberellin are extremely small, and treatment is not difficult. The effectiveness of gibberellin for induction of sprouting and its systemic properties in treated plants are revealed by the fact that vines sprayed during tuber maturation produce a high percentage of potatoes that are already sprouting at harvest (113a, 200).

Asparagus. "Positional" bud dormancy may also be broken in asparagus (*A. officionalis* L.) rhizomes. Application of large quantities of gibberellin to the stubs of the first-cut spears promotes more rapid growth and higher yields of spears from subsequently developing buds (149).

Seeds

Light- or temperature-conditioned dormancy in many seeds or parts of germinating seeds may be broken with gibberellin. With the tree peony (*Paeonia suffruticosa* Haw.), gibberellin replaced the need for low temperature pretreatment for the production of green shoots (11). It is the only chemical which has been found to break epicotyl dormancy in this species. Similarly, dormancy in both primary and secondary seed of wild oats (*Uniola latifolia* Machx.) may be broken with gibberellin, and it is the only chemical thus far tested which is effective. The effect of

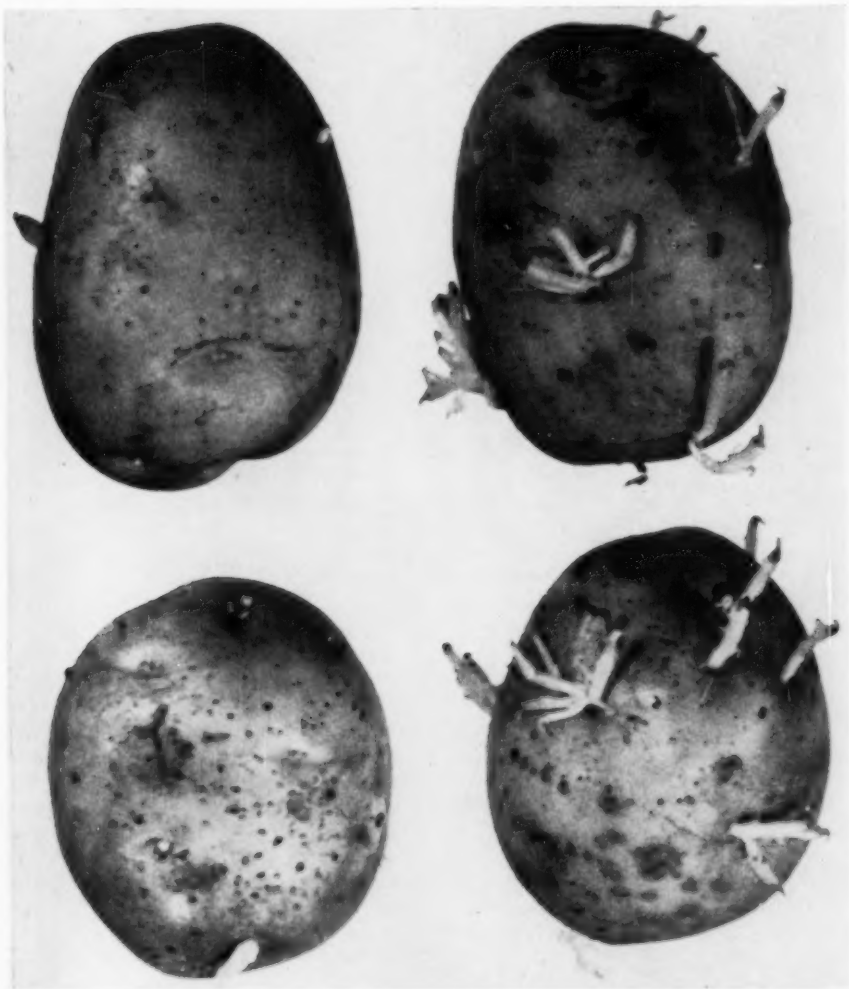


FIG. 13. The effects of gibberellin on sprouting in Katahdin potatoes. Left, control; right, treated with gibberellin. Note more uniform and rapid development of sprouts in treated tubers, resulting in earlier and more uniform crop emergence.

gibberellin on dormancy of wild oats may be an indirect means for its eradication in a single season (75). Newly harvested sorghum (*S. vulgare* Pers., *saccharatum* Boerl.), sudan (*Sorghum vulgare sudanense* Hitchc.) and Johnsongrass (*Sorghum halepense* Pers.) seeds exhibit varying degrees of dormancy. Gibberellin applied as a dust or slurry (¼ to ½ grams per 100 pounds of seed) has increased germination and improved stands (84). Old or stored cotton and cantaloupe seeds have been partially revitalized (84, 86). Germi-

TABLE XIII

RESPONSES OF CERTAIN WOODY ORNAMENTAL PLANTS TO FOLIAR SPRAYS OF GIBBERELLIN (13 WEEKLY APPLICATIONS OF 100 P.P.M. BEGINNING WHEN GROWTH WAS INITIATED IN THE SPRING). AFTER MCVEY AND WITTWER (135)

Plant	Annual growth responses to gibberellin				
	Successive flushes of growth	Delay setting of terminal bud	Increased number of nodes	Longer internodes	Stimulation of axillary buds
Euonymus fortunei vegetus (Rehd.)	x		x	x	
Magnolia Soulangeana (Soul.)	x			x	
Forsythia (Vahl.) "Arnold Dwarf"		x	x	x	
Phellodendron Amurense (Rupf.)		x	x	x	
Ligustrum obtusifolium (Sieb. & Zucc.) *vicari*				x	
Berberis thunbergi (DC) "Crimson Pygmy"				x	x

nation of seeds of *Arabidopsis thaliana* (L.) Heynh. and *A. Suecica* Fries (94), *Kalanchoë Blossfeldiana* (34), Grand Rapids lettuce (88) and a wild lettuce (*Lactuca scariola* L. (117)) is promoted by red light or a specific photoperiod. Gibberellin can either replace or partially substitute for the light requirement for germination in these seeds. The critical daylength for germination is lowered and the percent germination increased at all photoperiods when seeds of *K. Blossfeldiana* are treated with gibberellin.

An unusual use of gibberellin, not necessarily related to seed dormancy, may be in the barley malting industry. It is reported (142) that its addition to the steeping water promotes seedling germination, saccharifying activity, and hastens malt production.

Woody Plants

Dormancy and growth responses of woody plants during summer months may be modified by gibberellin in several ways. With some species there is a succession of growth flushes; with others, a delay in the setting of the terminal bud; node numbers may be increased, longer internodes formed, or growth of axillary buds stimulated (Table XIII). The increased growth of many woody plants following treatment with gibberellin is the result of a direct influence on summer and autumn dormancy. Often the effects of gibberellin parallel those of long days (4, 116, 135, 146). Growth may also be activated at temperatures below those that are normal for growth (116), and the winter rest may be broken or the cold requirement greatly reduced (44, 45, 52, 178). The practical implications afforded for extending the boundaries and seasons of production by reducing the cold requirement for normal growth and flowering in many woody ornamentals (Fig. 14) and tree fruits await further experimentation.

FIG. 14 (Opposite). Response of Sainte Therese hydrangea plants to cool storage and gibberellin. Left to right: plants unstored or stored 2, 4, or 6 weeks, respectively, at 4 to 5° C. Top row: plants without gibberellin. Second row: plants sprayed twice with 10 p.p.m. solution, 1 ml. per plant. Third row: plants sprayed four times with 10 p.p.m. solution, 1 ml. per plant. Bottom row: plants sprayed four times with 50 p.p.m. solution, 1 ml. per plant. (Photograph and legend, courtesy Dr. Neil W. Stuart, U.S.D.A., Beltsville, Maryland).

OTHER RESPONSES

Several additional responses to gibberellin, some indirectly influencing plant behavior, have been noted. The reversal of virus inhibition of vegetative growth induced by aster yellows in asters (*Callistephus chinensis* Nees.), corn stunt in sweet corn (*Zea Mays rugosa*), and wound tumor in Crimson clover (*Trifolium incarnatum* L.), as well as ring spot and yellows on the Montmorency cherry (*P. cerasus*) has been observed (79, 131). In no instance was the virus destroyed, but the dwarfing effects of the infections were partially or completely overcome. The mechanism of reversal of virus stunting has not been resolved.

According to Miller (138), a special use of gibberellin relative to virus yellows in the strawberry may be in stimulating runner growth that produces runner tip plants free of all except the latent A virus. Apparently no part of the yellows virus complex is inactivated but some components of the active virus do not move into the runner tip plants as fast as the stimulated cells divide. These observations, however, have not been confirmed (87).

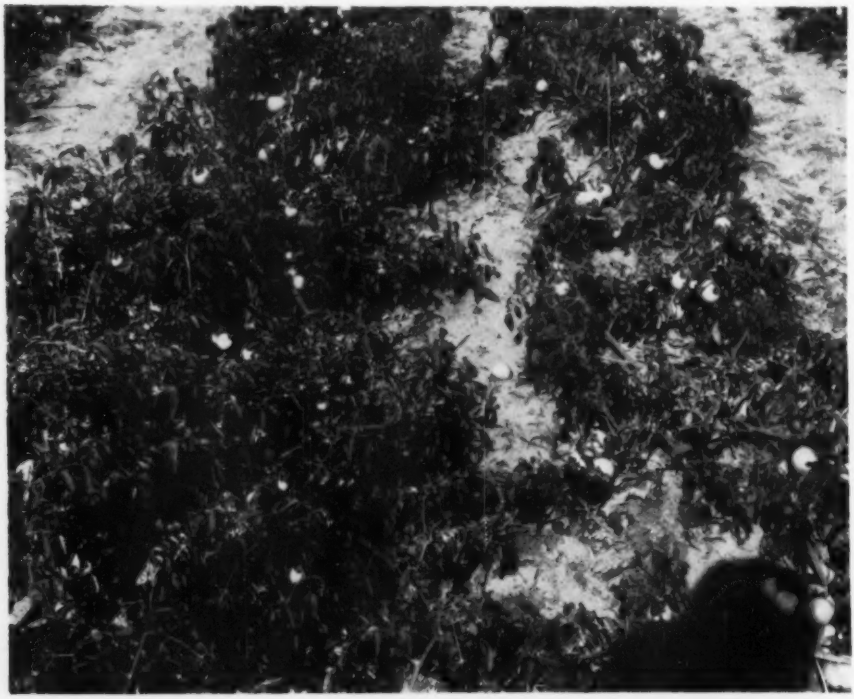


FIG. 15. Stimulating effects of gibberellin on the growth, flowering and fruiting of the tomato (var. Fireball). Plants in left row were sprayed with 100 p.p.m. of gibberellin on June 4 and 14; control row on right. Photographed (courtesy John Carew) July 29 at the Fred Lorentz farm near Benton Harbor, Michigan. Gibberellin-treated plants were larger and foliage was greener less damage from early blight (*Alternaria solani*). After Wittwer and Bukovac (197).

Reports on early blight (*Alternaria solani* Sorauer) of tomatoes are contradictory. A significant decrease in one case (12) and no effect in another (47) have been reported. Gibberellin may, however, have an indirect effect on early blight damage of tomatoes under field conditions (197). Apparently, treated plants are stimulated to grow and replace the diseased foliage more rapidly and give the appearance of reduced infection (Fig. 15). Information is nonconclusive as to the effects of gibberellin on *Fusarium* wilt (*F. lycopersici* Sacc.) of tomatoes (51).

Preliminary tests indicate that gibberellin-treated bean plants may no longer serve as functional hosts for spider mites (*Tetranychus telarius* L.) (54), and that "in-the-row" or soil applications of gibberellin might alter growth and reproduction of soil microflora (14, 128, 199a). Other studies concerned with the effects of gibberellin on the herbicidal action of 2,4-D suggest that prior treatment of bean plants with gibberellin increases the absorption-transport rate of 2,4-D (8), while simultaneous treatment of grass in early spring results in no loss of the growth-promoting properties of gibberellin but the herbidical action of 2,4-D on broad-leafed weeds is largely negated (67). Gibberellin completely counteracts the growth-inhibiting effects of 2,3,5-triiodobenzoic acid (4a) but only partially that induced by maleic hydrazide (23, 24). Greater susceptibility to freezing has been reported for gibberellin-treated celery (132a), and it has been observed that autumn-treated rye subsequently showed severe winter injury (200).

EFFECTS OF GIBBERELLIN ON PLANT COMPOSITION

Studies of the effects of gibberellin on plant composition have accompanied some of those that have dealt with growth, flowering and fruiting responses (18, 43, 74, 76, 141, 152, 177, 187, 195). In only a few instances have differences in mineral, organic constituents, and dry matter contents been significant (76, 141, 149a, 177, 195). In Kentucky bluegrass total sugars were decreased, but this was not true of Utah 10-B celery (Table XIV).

It has been reported by Morgan and Mees (141) that protein content of gibberellin-treated grass in Britain was reduced by one half to two percent, but this was not confirmed by studies in Michigan (195).

Both increases (18, 76) and decreases (74, 76, 187, 195) in total sugars have been reported depending upon the crop and the time of treatment. Thus far, yields of sugar beets and sugarcane have not been significantly increased without corresponding reductions in percent sucrose (40, 42, 43, 73, 152, 177). It should be possible, however, by proper timing of gibberellin treatments, that the

TABLE XIV

EFFECT OF GIBBERELLIN ON THE COMPOSITION OF *Poa pratensis* L. (KENTUCKY BLUE) AND *Apium graveolens* L. (UTAH 10-B). AFTER WITTWER, BUKOVAC AND GRISBY (195), AND HELLMAN, SELL, WITTWER AND BUKOVAC (76)

Constituent	Kentucky bluegrass		Utah 10-B celery	
	Control	Gibberellin	Control	Gibberellin
Dry matter	22.8	21.9	17.5	22.8
	(*Percent of dry matter*)			
Total sugars	8.65	6.09	4.00	5.29
Nitrogen	3.60	3.52	5.06	5.65
Potassium	3.2	3.0	...	...
Phosphorus	0.36	0.37	0.64	0.54
Calcium	0.50	0.50	2.05	2.79
Magnesium	0.19	0.18	0.21	0.21
Iron	0.0091	0.0084	0.0089	0.0075
Manganese	0.0029	0.0028	0.0046	0.0041
Zinc	0.0025	0.0025	0.0041	0.0041
Copper	0.0017	0.0017	0.0062	0.0036
Boron	0.0012	0.0011	0.0060	0.0025

TABLE XV

COMPARATIVE ELONGATION OF EPICOTYLS OF *Phaseolus vulgaris* L. (BLUE LAKE BEAN) 24, 48, 72 AND 96 HOURS FOLLOWING THE APPLICATION OF 10 MICROGRAMS OF GIBBERELLIN A_1, A_2 AND A_3 TO THE STEM APEX AND TO THE LEAF BLADE. AFTER BUKOVAC, WITTWER AND GAUR (28)

Hours after treatment	Control (No treatment)	Gibberellin A_1		Gibberellin A_2		Gibberellin A_3	
		Stem apex	Leaf blade	Stem apex	Leaf blade	Stem apex	Leaf blade
		(*centimeters*)					
24	1.0	1.8	1.6	1.7	1.1	1.8	1.5
48	1.8	6.1	5.1	6.0	2.6	6.3	5.3
72	3.3	15.6	11.4	14.2	4.5	16.2	13.4
96	5.2	28.6	17.6	22.1	6.7	31.8	23.1
Means *	2.8	13.0	8.9	11.0	3.7	14.0	10.8
Ratio **		1.46		2.97		1.30	

* L.S.D. between means at the 5% and 1% levels = 1.56 and 2.05, respectively.
** Ratio between the mean of epicotyl growth (elongation) following stem apex and leaf blade applications for all times.

greater photosynthizing surface which often results might be effective in greater carbon dioxide fixation and result in the accumulation, at least in some environments, of greater quantities of sucrose in sugar-producing plants. This appears all the more likely in that the protein content of treated plants may also be reduced (141). Results of some experiments with sugarcane and sugar beets look encouraging (40, 43, 73, 152, 177). Strangely enough, the remarkable increases in yields of seedless grapes are not accompanied by significant decreases in soluble solids or other important components (186, 187). Similarly, promotion of fruit setting and development in other crops does not appear to impair edible quality or induce significant changes in food value (16, 45, 46, 77).

Chemical residues in treated food crops may well be discussed relative to the effects of gibberellin on plant composition. Since gibberellins, or substances similar to the gibberellins, have now been extracted from a large number of economic species, it may well be that gibberellins occur in all intact plants, many of which are indistinguishable or identical with those produced by *Gibberella fujikuroi*. Crops treated with gibberellin and used as feed have had no effect on test animals (183), and the pure chemical in massive dosages has resulted in no pathological symptoms (150).

COMPARATIVE BIOLOGICAL EFFECTIVENESS OF THE GIBBERELLINS

The comparative biological activities of the various gibberellins and two methyl-ester derivatives have been studied relative to several crop responses (28, 29). These have included epicotyl elongation in the bean, dry matter accumulations in celery, stem elongation and flowering in lettuce and dill, and parthenocarpic fruit setting and development in tomatoes. The following order of activity has been established: $A_3 > A_1 \cong A_4 > A_2 >$ methyl-ester $A_1 \cong$ methyl-ester A_3. Some of these

FIG. 16 (Opposite). Epicotyl growth responses 48 hours after applying 10 micrograms of gibberellin A_1 (top), A_2 (center) and A_3 (bottom) to one of the primary leaves of the bean. Left to right, absorption-transport periods of 6, 12, 24 and 48 hours, respectively, established by removal of the gibberellin treated leaves.

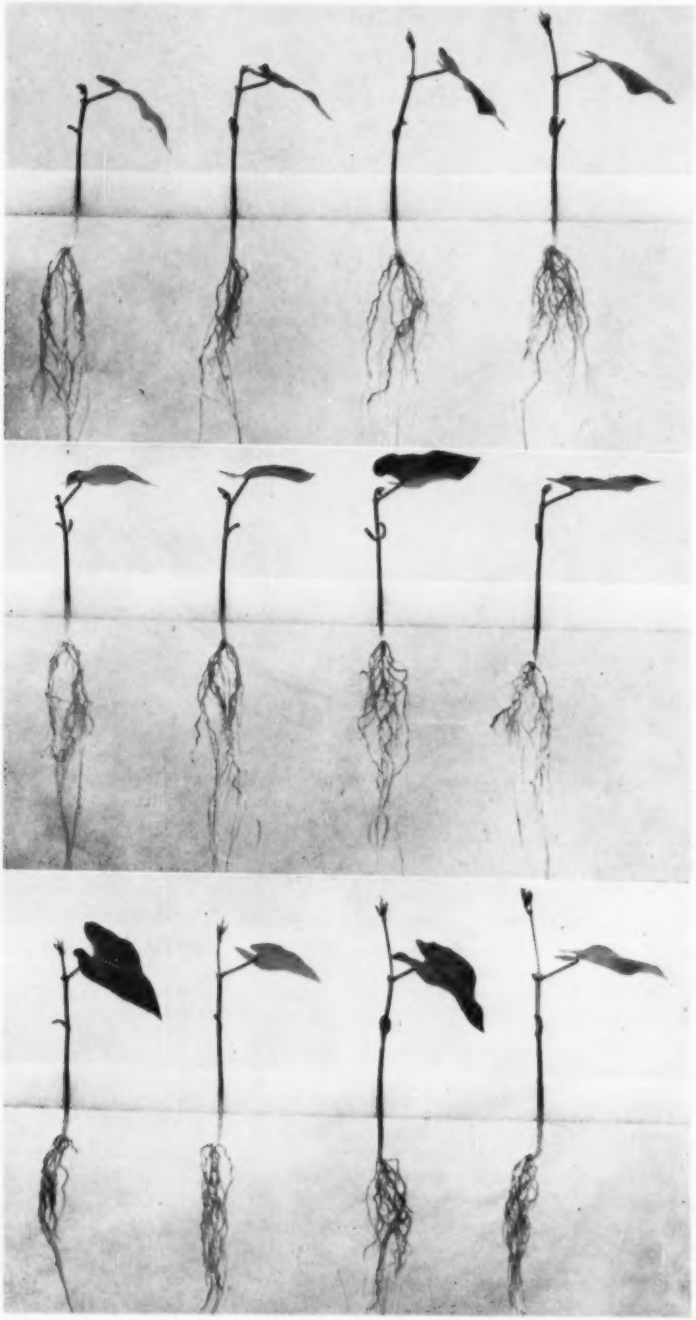


FIG. 17. Comparative effects of gibberellins A_1, A_2, A_3 and the methyl esters of A_1 and A_3 on seedstalk elongation and flowering in Great Lakes head lettuce. Left to right: Control (not treated), A_1, methyl ester of A_1, A_2, A_3, and methyl ester of A_3. Ten microliters of a 3-millimolar solution of each chemical applied 3 times to plant apices at 2-week intervals.

relationships are illustrated by Figures 16 and 17.

When equal amounts of gibberellins A_1, A_2 and A_3 are applied to the stem apex of bean seedlings, significant and comparable elongation occurs. By contrast, gibberellins A_1 and A_3 applied to one of the primary leaves of the bean produce significantly longer epicotyls than A_2 (Fig. 16 and Table XV). This has suggested a limitation in absorption-transport of gibberellin A_2.

Excepting those studies directly associated with comparative biological evaluations of the gibberellins, or their derivatives, all experiments thus far conducted with gibberellin and reviewed in this paper have been with A_3 (gib-

TABLE XVI

COMPARATIVE ACTIVITIES OF AUXIN, KINETIN AND GIBBERELLIN APPLIED TO INTACT PLANTS (+ PROMOTES, – INHIBITS, 0 NO EFFECT, ( ) SLIGHT EFFECT, ? NO DATA)[1]

Responses	Auxin	Kinetin	Gibberellin	Gibberellin references
Cell elongation	+	+	+	Too numerous to list
Stem elongation	(+)	(+)	+	Too numerous to list
Cell division	+	+	+	17, 60, 166
Root growth	–	?	– or + or 0	18, 20, 49a, 90, 163, 188a
Root formation	+	+	–	20, 21, 49a, 90
Callus formation	+	+	0	89
Shoot formation	+	+	0	21
Lateral bud growth	–	+	+	20, 23, 44, 49, 68, 89, 90, 92, 126, 132a, 135, 179a, 200
Leaf expansion	–	(+) or (–)	+	65, 79a, 92, 95, 96, 132, 132a, 152
Leaf abscission	–	0	0	20, 99
Leaf epinasty	+	0	0	89
Flower formation:				
Day neutral plants	+	0	(–) or (+)	26, 132, 132a, 159, 190, 191, 197
Biennial plants	0	0	+	15, 25, 37, 50, 62, 63, 64, 100, 101, 102, 103, 111, 113, 134, 169, 177, 189, 190, 192
Long-day plants	(+)	0 or (–)	+	27, 30, 31, 32, 71, 72, 101, 102, 103, 104, 109, 111, 118, 119, 123, 127, 192, 193, 198
Short-day plants	(–)	0 or (+)	(+) or (–) or 0	35, 36, 66, 69, 70, 70a, 101, 102, 108, 110, 126, 178, 198
Monoecious plants	(+)	0	(–)	144, 197, 200, 203
Flower size	0	?	+	48, 49, 110, 112, 135, 178
Breaking of dormancy	0	?	+	11, 44, 45, 52, 68, 75, 84, 94, 113a, 116, 160, 162, 181, 182
Seed germination	0 or –	(+)	+	34, 75, 88, 94, 117, 139, 142, 196
Fruit setting	+	0	+	16, 45, 77, 151, 159, 169a, 172, 173, 174, 184, 185, 186, 187, 190, 191
Overcoming dwarfism:				
Genetic	0	0	+	3a, 18, 19, 22, 24, 56, 86, 153, 177, 191
Physiologic	0	?	+	10, 147
Dry matter accumulation	0	(+)	+	3, 18, 24, 43, 61, 65, 73, 80, 106, 132a, 140, 141, 159, 177, 178, 180, 190, 194, 201
Nonphotosynthetic growth of *Lemna minor*	0	+	0	78
Vegetative growth in short days	0	0	+	18, 42, 80, 178, 201
Vegetative growth at low temperature	0	0	+	42, 43, 61, 80, 106, 116, 141, 194, 195

[1] A plus or minus sign should not imply that these effects are found in all plants but that an effect has been observed; usually in a majority of the cases examined. Auxin and kinetin effects on cell and stem elongation, cell division, shoot formation, lateral bud growth and callus formation are usually more pronounced on decapitated plants or excised plant parts where the native source is removed or limited. The frequent no effect or slight effect from kinetin may in some instances result from limited uptake since absorption and transport probably occur less readily than with auxin or gibberellin. Literature citations are given only for gibberellin, and in some instances for kinetin where the effects are not general or well known. The suggestions of Dr. Anton Lang, Dept. of Botany, Univ. Calif. at Los Angeles pertaining to certain aspects of this table are acknowledged.

berellic acid), potassium gibberellate or a mixture of A_1 and A_3.

CONCLUSIONS

The favorable modifications of plant behavior resulting from treatment with gibberellin may well exceed the anticipation of those who have been most active in developing its potential agricultural uses. Yet, no one is able to predict its ultimate value at this time. Several uses (Table XVIII), some already well advanced commercially, may place this unique group of native plant growth substances on a par with all, including the herbicides, that have evolved from the auxin group of plant growth-substances. This should follow if versatility of induced responses is any criterion (Tables XVI, XVII and XVIII).

A perusal of Tables XVI, XVII and XVIII suggests that gibberellin has for many plant responses served as a major scientific breakthrough for the horticulturists, the agronomists, the plant physiologists and perhaps even the plant pathologists. Only with this consideration in mind can one evaluate gibberellin in terms of its future potentialities in crop production. It offers a means of controlling important responses heretofore, at least on intact plants, not easily subject to chemical regulation. These include elimination of dwarfism, reversal of virus stunting, elongation of stems, expansion of leaves, increased production of dry matter, acceleration of flowering in biennials and long-day annuals, promotion of uniformity in growth, flowering and fruiting, increased flower size, control of fruit size and maturity, reduction or replacement of cold and photoperiodic requirements for growth and flowering, and promotion of normal growth rates at suboptimal temperatures.

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(*Continued on page 248*)

TABLE XVII

TWENTY-FIVE PHYSIOLOGICAL RESPONSES IN SELECTED HIGHER PLANTS CONTROLLED BY GIBBERELLIN HERETOFORE NOT SUBJECT TO CHEMICAL REGULATION

Physiological response	Plants responding	References
Stem elongation in light	Most plants	2, 5, 10, 18, 20, 23, 24, etc.
Reversal of genetic dwarfism	Peas, beans, corn, tomatoes, cotton, sugar beets, coffee	19, 21, 24, 56, 86, 153
Reversal of physiologic dwarfism	Apple and peach	10, 147
Provokes climbing habit	Bush beans and wild lettuce	124
Reversal of virus stunting	Clover, asters, corn, cherry, strawberry	79, 131
Induction of flowering in cold-requiring biennials in absence of cold	*Centaurium*, *Hyoscyamus*, carrot, foxglove, stocks	15, 25, 37, 50, 102, 111, 113, 190
Acceleration of flowering in cold-requiring biennials receiving partial cold	Sugar beets, rutabagas, collards, turnips, celery, cabbage, kale, pansy	25, 62, 63, 111, 134, 169, 177, 189, 190, 192
Induction of flowering in obligate long-day annuals grown in short days	*Lapsana*, *Samolus*, *Silene*, *Rudbeckia*, endive, spinach, pyrethrum	31, 32, 101, 102, 192, 193, 198
Acceleration of flowering in facultative long-day annuals grown under either long or short days	*Adonis*, *Arabidopsis*, *Bryophyllum*, dill, lettuce, mustard, Chinese cabbage	27, 30, 32, 33, 193, 198
Acceleration of flowering of a facultative short-day plant grown in long days	*Cosmos*	198
Accelerated flowering under short days or reduction of photoperiodic cycles of obligate short-day plants for full flowering response	*Xanthium*, *Chrysanthemum*	35, 36, 66, 108, 178
Increased staminate-pistillate flower ratio in cucumbers	Pickling and slicing types	200 and this report
Reversal of inhibition of growth and fruiting during "cut-out"	Cotton	181, 182
Increase of flower size	*Hydrangea*, geranium	48, 110, 112, 135, 178
Promotion of flower opening	Coffee	3a
Increase of berry size beyond that possible by girdling or any other growth substances	Black Corinth and Thompson Seedless grapes	186, 187
Increase in leaf area or photosynthesizing surface	Beans, peas, cucumbers	18, 22, 49, 65, 95, 96, 199
Increase in total dry matter and photosynthates	Wheat, grasses, peas, celery, beans, etc.	3, 18, 22, 24, 43, 65, 132, 132a, 140, 141, 152, 159, 177, 178, 190, 201
Reduction in cold requirement for normal growth and flowering responses	*Hydrangea*, Elberta peach	50, 178
Partial replacement of effects of long days in promotion of vegetative growth and dry matter production	Celery, grasses, rhubarb, peas, sugarcane	5, 43, 80, 116, 135, 146, 200, 201
Replace or reduce primary light requirement for seed germination	*Arabidopsis*, *Kalanchoë*, lettuce	34, 88, 94, 117
Promotion of growth in dormant seed	Wild oats, tree peony	11, 75
Replace or partially substitute for long days in growth of woody ornamentals	*Camellia*, red oak, Japanese maple, sumac	116, 135, 146
Promotion of growth or seed germination at subnormal temperatures	Grass, sugarcane, cotton, peas, beans, corn	5, 42, 43, 61, 80, 84, 86, 106, 116, 140, 141, 194, 196
Promotion of simultaneous growth in lateral and terminal buds	*Citrus*, lettuce, beans, peas, snapdragon, tobacco, potato tubers	23, 44, 49, 68, 132a, 135, 200

TABLE XVIII

PROMISING USES FOR GIBBERELLIN IN CROP PRODUCTION
(NOT TO BE CONSTRUED AS RECOMMENDATIONS)

Crop	Response	Gibberellin treatment	Beneficial effects	Limitations or deleterious effects	References
Annuals (long-day)	Flowering	Spray growing tips weekly with 10 to 1000 p.p.m.	Earlier flowering and seed production	Taller plants, weaker seed-stalks	27, 30, 31, 32, 71, 72, 101, 102, 103, 104, 109, 111, 118, 119, 123, 127, 156, 157, 192, 193, 198
Biennials (cold requiring)	Flowering	Spray growing tips weekly or at alternate weeks with 100 to 1000 p.p.m.	Earlier flowering and acceleration of seed production for variety improvement	Taller plants, weaker seed-stalks, seed setting may be reduced	15, 25, 37, 50, 62, 63, 64, 100, 101, 102, 103, 111, 113, 134, 169, 177, 189, 190, 192
Beans, peas, cotton, small grains	Germination and seedling emergence	Slurry or dust to seed 5 to 50 mg./lb.	Earlier emergence	Weaker hypocotyls, reduction in stand	7, 14, 57, 82, 86, 137a, 139, 196
Celery	Maturity and vegetative growth	Foliage spray 3 to 15 grams per acre 3 weeks before harvest	Earlier maturity, longer stalks, higher yields	Harvest more critical, holding and market quality may be reduced, moisture and fertilizer requirement increased	9, 91, 149, 180, 197
Citrus	Fruit setting and development	Spray flowers or small fruit 250 to 1000 p.p.m.	Greater fruit set, improved color	.....	40a, 77, 169a
Coffee	Flower opening	Spray flower buds 3 to 4 mm. in dia. 1 to 20 p.p.m.	Promotes uniform flower opening and maturity, reduces labor in harvest	.....	3a
Corn	Male sterility	Spray plants when immature tassels are 4–6 cm. 500 to 1000 p.p.m.	Sterile tassels for hybridization of inbred lines	.....	144, 197
Cotton	Vegetative and fruiting	Spray open flowers 1 to 100 p.p.m. or 1 to 6 grams per acre	Reversal of "cut-out" phenomenon	Smaller bolls and fewer seeds in bolls	181, 182
Calimyrna figs	Fruit setting and development	Spray trees 25 to 1000 p.p.m.	95 to 100% parthenocarpic fruit setting and earlier maturity	Rest period of terminal buds broken	45
Geranium	Flowering	Spray opening buds with 1 to 10 p.p.m.	Larger flowers that last longer	Flower stalk elongation	48, 110, 112

TABLE XVIII (*Continued*)

Crop	Response	Gibberellin treatment	Beneficial effects	Limitations or deleterious effects	References
Grapes (seedless)	Fruiting and fruit setting	Spray post-bloom or at berry set with 8 to 20 grams/acre (5 to 20 p.p.m.)	Increased set and size of clusters and berries, looser clusters	.....	172, 173, 174, 184, 185, 186, 187
Grapes (seeded)	Fruiting and fruit setting	Spray at post-bloom 10 to 100 p.p.m. or 4 to 16 grams/acre	Increased set and size of clusters and berries, better color	.....	186, 187
Grasses	Vegetative growth	Spray in early spring, winter or autumn 5 to 50 grams/acre	Growth stimulated, yields increased, and dormancy broken during cool temperatures and low light	Thinner stands, repeat applications necessary for substantial increases in yield	61, 80, 106, 137a, 140, 141, 194, 199
Ornamentals (woody)	Vegetative growth	Spray weekly or alternate weeks 10 to 100 p.p.m.	Greater growth, increased size	Additional fertilizer may be needed, plants may be more susceptible to winter injury and drought	4, 135, 156, 157
Ornamentals (herbaceous)	Vegetative growth	Spray weekly or alternate weeks 10 to 100 p.p.m.	Greater growth, increased size	Additional fertilizer may be needed, plants may grow excessively tall	156, 157
Peach	Breaking dormancy	Sprays of 200 to 4000 p.p.m.	Reduces chilling requirement, may extend peach growing further south	.....	52
Pears (Bartlett)	Fruit setting	Spray at full bloom with 1 to 100 p.p.m.	Increased fruit set	.....	16
Potatoes	Breaking dormancy, and growth of sprouts from seed pieces	Dip or spray seed pieces in solution of 0.25 to 1.0 p.p.m. or 1 to 2 grams/10 tons	Earlier and more uniform plant emergence	Excessive stolon elongation	129, 160, 162
Spinach	Stimulating vegetative growth and re-growth	Spray young plants or after cutting with 25–50 p.p.m. or 5–10 grams/acre	Greater growth and yields during fall and winter	Growth of seedstalks may be stimulated during spring and summer	137a, 200
Stocks	Flowering	Spray foliage or growing tips weekly with 100 to 500 p.p.m.	Earlier and out of season flowering	Flower stalks may be too elongated	109, 111, 113
Wild oats	Breaking dormancy of seed	Seed soaked in solution of 50 p.p.m.	Breaking of seed dormancy to enable eradication	Field application may be difficult	75

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NOTE

The footnote to Table XI on page 229 should read as follows:

* Least differences necessary for significance between any two values at the 9-hour photoperiod P .05 = 10.8, P .01 = 14.9; for the 18-hour photoperiod P .05 = 12.3, P .01 = 17.0, respectively.

Caro-Red, a New Provitamin A Rich Tomato[1]

The development and release of a new tomato variety which produces fruit containing approximately ten times the provitamin A content of common red tomatoes is announced. The beta-carotene values for Caro-Red are within the lower ranges reported for carrots. Present consumer usage of a variety such as Caro-Red will most likely be confined to use as a garden type where additional variety and flavor are desired.

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Perhaps the most widespread utilization of plant introductions has been by the pathologist or breeder intent on improving the disease resistance of various commercial crops. In the tomato, for example, many of the wild species have been used as sources of resistance to various tomato diseases (3), and these efforts are continuing in a more systematic search for additional sources of disease resistance which might be of potential value in tomato improvement (1). Surveys for other potentially useful genetic characters have been more limited, possibly because the goals or benefits to be achieved are less precisely defined or because the assay techniques are less obvious.

The work reported here is of added interest in that the original crosses, made with the goal of transferring disease resistance from the wild parent, resulted in certain aberrant pigment types. When these were analyzed chemically, the potential value of the material was realized; and a survey was made to determine the genetic variability of the genus with regard to provitamin A content (5).

From the progeny of crosses between common red canning tomatoes, *Lycopersicon esculentum* Mill., and the wild species, *L. hirsutum* Humb. and Bonpl., Lincoln *et al.* (5) and Kohler *et al.* (4) isolated a new pigment type which was distinguished from common tomatoes by producing orange fruits in which most of the carotene produced was *beta*-carotene. More recently similar pigment types have been derived from other *Lycopersicon* species by Mackinney *et al.* (7), and by Soost (9).

The first genetic investigation of these types by Lincoln and Porter (6) indicated that strains which produced *beta*-carotene to the near exclusion of lycopene differed from a common red canning type by a single, pigment-controlling genetic factor *B* which lacked dominance. That this explanation was inadequate was first noted by Tomes *et al.* (10) when it was found that certain selections which produced intermediate quantities of lycopene and *beta*-carotene bred true and that recombinants were found among the progenies of certain of the high *beta* orange selections. Subsequent study (11) showed that *B* is a dominant gene and that the intermediate nature of the F_1, as well as the F_2 distribution, depends upon the interaction of the dominant gene *B* and a recessive

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modifier mo_B[2]. The highest level of provitamin A is achieved when *BB* or *BB'* are in combination with the recessive mo_Bmo_B These genotypes produce fruits which have orange-colored flesh. Intermediate provitamin A levels are produced when the two dominants *B* and mo_B' are found together in the genotype. In such plants the fruits are orange-red internally. With respect to these two loci, these intermediate types differ from common red tomatoes by the single pigment-controlling factor *B*.

The present paper reports the development and release of a new tomato variety which produces fruit containing approximately ten times the provitamin A content of common red tomatoes. This new variety is of the intermediate type described above. The external color of the fruit is orange, and in superficial appearance it resembles the color of existing orange varieties such as Sunray or Jubilee. The flesh color is orange-red, differing from existing varieties. To the eye this internal color is intermediate between the orange of Jubilee and the red of standard varieties. The name Caro-Red has been chosen as being descriptive of both the high carotene content and the carrot-like, orange-red color.

It should be noted that the orange and orange-red *beta*-carotene producing strains described above are entirely separate and distinct from the yellow and the tangerine orange types both genetically and chemically (10). Neither the yellow (*r r*) nor the tangerine orange (*t t*) type (e.g., Jubilee) contains more provitamin A than common red tomatoes.

Derivation of Caro-Red

The original cross involved the wild, green-fruited species *Lycopersicon hirsutum*, P.I. 126445. The pedigree includes two early crosses involving the variety Indiana Baltimore and four crosses involving Rutgers. The pedigree method of individual plant selection was used throughout. The release stock is a bulk multiplication of two individual plant selections from the eighth selfed generation following the last cross. Because of the parentage, Caro-Red most nearly resembles Rutgers with the exception of fruit color. The fruit is a deep globe of comparable size (figure 1), and the internal structure of the fruit is reasonably fleshy (figure 2). The vine is of standard length, but the foliage is somewhat lighter in density than that of Rutgers. In terms of maturity, Caro-Red is of the same season as Rutgers.

The Provitamin A Content of Caro-Red

In a red tomato variety such as Rutgers, about 95 percent of the total carotene pigment found in the fruit is lycopene, the common red-tomato pigment. Much of the remaining pigment is *beta*-carotene, the precursor of vitamin A. In Caro-Red the intermediate color is the result of a different mixture of these same two carotenes, in which *beta*-carotene predominates. In several determinations this past season, Caro-Red produced an average total carotene content of 66.3 micrograms per gram fresh weight, of which an average of 44.2 was *beta*-carotene. Under comparable conditions, Rutgers produced slightly higher total carotene values (78.8 micrograms) but averaged only 5.3 micrograms of *beta*-carotene per gram. Over a period of several seasons, Caro-Red has averaged approximately ten times the provitamin A content of the red variety Rutgers. These *beta*-carotene values for Caro-Red are within the lower range reported for carrots (8), generally considered an excellent source of provitamin A. On the basis of these data, a single

[2] The symbols mo_B' and mo_B are used here in place of the I^B and i^B previously used in order to conform with the recently published rules of nomenclature in tomato genetics (2).

fruit of Caro-Red would provide from one and a half to two times the recommended daily vitamin A allowance for an adult.

Yield Comparisons

The yield of marketable fruit from the variety Caro-Red has compared favorably with the yields of standard varieties in replicated yield trials at Lafayette. In an eight-replicate trial, under the ideal conditions of the 1956 season, Caro-Red averaged 28.6 tons of marketable fruit per acre, Rutgers averaged 26.1 tons per acre, Short Stemmed Boone, 28.3 and Purdue 1361, 24.5 tons (L.S.D. at .05 = 2.6). In a six-replicate, 1957 trial, under more normal conditions, Caro-Red averaged 13.3 tons per acre, Rutgers, 12.6, Purdue 1361, 14.6 and Urbana, 13.6 tons per acre (L.S.D. at .05 = 2.4). These results suggest that Caro-Red produces yields comparable to but not significantly better than the variety Rutgers and not grossly different from the other named varieties included in these trials.

FIG. 1. Mature fruit of Caro-Red on the vine.

Flavor Evaluation

Since Caro-Red represents a new tomato type both genetically and chemically, a critical flavor evaluation was undertaken this past season. The trial was conducted by an impartial observer, Mr. Andrew Radkins, of the Department of Psychology, Purdue University. Mr. Radkins' primary interest in the project was in the technique of conducting and statistically analyzing tests of this type. The problem served as a vehicle for a graduate research problem in statistical design.

The taste trial was conducted at the Indiana State Fair with over 3,000 individuals participating. A special light-tight, air-conditioned booth was set up, where color differences could be masked with the use of filtered light. Two gen-

eral types of trials were conducted: 1) difference tests and, 2) preference tests. In color-masked, randomized, triangular difference tests, the subjects were asked to select the different sample in comparisons between Caro-Red and Rutgers, Caro-Red and Kokomo, and Caro-Red and Sunray. Preference tests were also conducted in color-masked and unmasked paired trials involving the same variety comparisons.

FIG. 2. Whole and sliced fruit of Caro-Red (left) and of Rutgers (right).

Briefly stated the results were as follows: Caro-Red has a distinct or different flavor. A statistically significant number of people selected the odd or different sample in tests involving all three of the varieties included. Thus, the flavor is distinct from that of Kokomo, Rutgers, or Sunray. In paired preference tests, 46.9% preferred the distinct flavor of Caro-Red to Rutgers, 45.9% preferred the new flavor to that of Kokomo, and 41.6% preferred the new flavor to that of Sunray. Of these, only the Sunray data deviate significantly from the hypothesis of equal preference. Preferences for Caro-Red were somewhat less when color was not masked in the tests involving Rutgers and Kokomo, indicating a color preference for red.

Potential Use of Caro-Red

Since Caro-Red is a new tomato which differs from common varieties especially in color, it is not anticipated that Caro-Red will find ready acceptance in commercial canning either as a juice or whole pack type. Color competition with the attractive red varieties may preclude this possibility. Work by Dr. N. W. Desrosier and Dr. G. R. Ammerman of the Food Technology section, Department of Horticulture, Purdue University, indicates that tomatoes of the Caro-Red type may have use possibilities in areas where preconceived color ideas do not rule out acceptance. Their work indicates that Caro-Red and similar types

make excellent oil-free salad dressings and that they might be used to advantage in soups or as dressings or sauces in prepared foods.

Present consumer usage of a variety such as Caro-Red will most likely be confined to use as a garden type where additional variety and flavor are desired. Orange types such as Jubilee and Sunray have found limited aceptance in this area. Caro-Red has the additional advantage of high vitamin content.

Summary

Caro-Red is a new provitamin A rich tomato variety which is distinct from commercial types presently grown. The external color of the fruit is orange, and in superficial appearance it resembles the color of existing orange varieties such as Sunray or Jubilee. The flesh color of Caro-Red is orange-red, differing from existing varieties. The fruit contains approximately ten times as much *beta*-carotene as the variety Rutgers. The *beta*-carotene values reported for Caro-Red are within the lower range reported for carrots, generally considered an excellent source of provitamin A.

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The Natural History of Jojoba (*Simmondsia chinensis*) and Its Cultural Aspects

Simmondsia chinensis *is unique in many ways. Endemic to the Sonoran Desert of Mexico and the United States, its broad, persistent, heavy leaves are unlike any of its associates. Its large edible seeds contain about 50% oil, which is directly used as a cooking oil and as a hair oil. The oil has excellent qualities for many industrial and medicinal uses. Chemically it is a liquid wax and by hydrogenation is easily converted to a hard white wax. Jojoba's singular characteristics as a desert shrub, however, present many problems facing its development as a cultivated plant.*

HOWARD SCOTT GENTRY *

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Introduction

Jojoba, the gray box bush, is a drought-resistant, long-lived, evergreen, desert shrub bearing fruits like an acorn set in sepals. Usually bushy, it may grow to three meters in stature or mature only as a low mound two to five decimeters tall, depending upon its environment (Figs. 1, 2). The natural life span appears to be over 100 years and may exceed 200 years. A stem of a wild shrub four to five centimeters in diameter shows over 85 annual rings. This grew in the arid San Matias Pass of Baja California, where a year may pass without rainfall. It is, therefore, a shrub in space and a tree in time; *Simmondsia chinensis* (Link) Schneid. in botany.

Several writings have appeared on jojoba during the last 25 years announcing the presence of a liquid wax in the seed, its potential in industry, and the possibilities of the shrub as a cultivate (7, 8, 10, 12). More recently, Daugherty, Sineath, and Wastler (5) presented their survey of jojoba as a potential raw material source for industry. They fairly established an economic potential for the product. Because of limited information, however, much of the real character of the plant and its problems in cultivation have remained obscure. The following account presents in a brief or generalized way the writer's study of the plant as a field subject together with his limited knowledge of the few attempts to cultivate it. The observations are based primarily upon a field study from March to October 1957 and upon less intensive periods of observation between 1946 and the present.

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Wild Jojoba

The Natural Area. The natural area of jojoba is shown in Fig. 3 and comprises approximately 100,000 square miles between latitudes 25° and 31° North and between longitudes 109° and 117° West. This area closely approximates that of the Sonoran Desert as defined by Shreve (13). The population incidence within this area varies from a few individuals to 200 per acre. There are many small separate populations covering few to many acres and some extensive massive populations with millions of individual plants, as along the slopes of the Pinal Mountains of Arizona and upon the high desert plain of San Matias Pass in Baja California. In the Sonoran Desert jojoba occupies elevations between 2000 and 4000 feet, rarely going lower. It can be expected in the Sonoran Desert mountains generally between these altitudes, but it is lacking over large extents of plains and valleys. In Baja California (Fig. 4), however, it occurs down to sea level along the outer coast, in an environment outside the limits of the Sonoran Desert. This species extends as far south as the peninsular cape district, where it meets, but does not enter, the Tropical Short-tree Forest. Although jojoba has a wide ecologic range from sea level to 4000 feet altitude, its intolerances restrict it to specific habitats within the region. The plants are completely lacking in areas which appear ideally

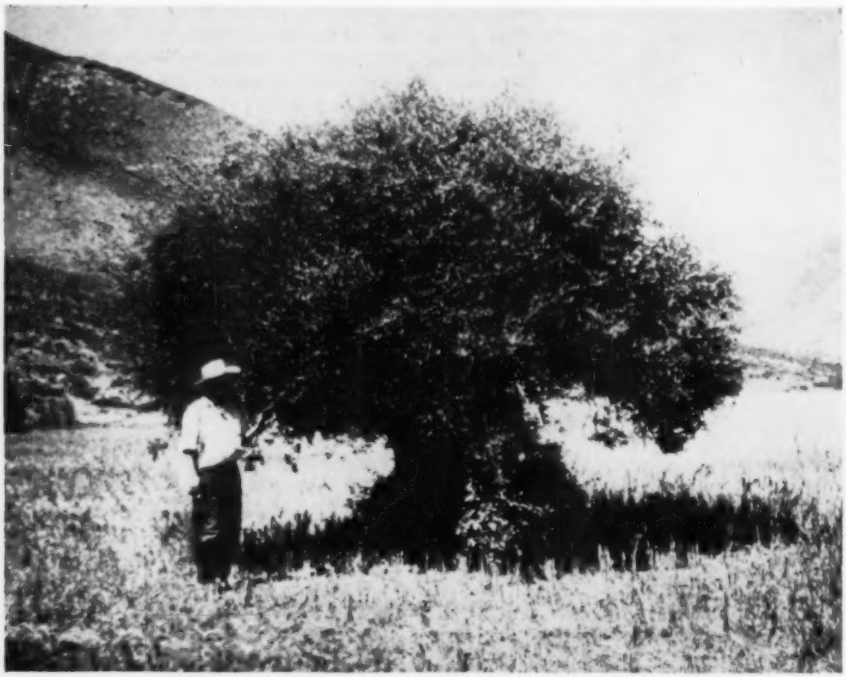

FIG. 1. A very large male plant of jojoba in the Calentura valley of Baja California. The "trunk" is composed of many intertwined stems. The lower foliage has been browsed.

suitable, as the open sandy table land between Cave Creek and Camp Creek in Arizona, and on the equable open slopes about Ramona, California, where the same plant association occurs that characterizes its environment a few miles southward. Jojoba is, therefore, definitely selective of sites and the following observations will further define its ecologic position.

FIG. 2. The low coastal form of jojoba growing with *Agave shawii, Rosa minutifolia, Lycium* sp. and others near San Telmo, Baja California.

The Environment. Jojoba is usually restricted to well-drained, coarse, desert soils, as the sandy alluviums and coarse atrital mixtures of gravels and clays derived from such igneous materials as granitics and volcanics (Fig. 5). Such sites are well-aerated. It is also found on sedimentary formations composed of such materials, usually geologically young, as the San Diego Terrace, the Gila Conglomerate, and the Beaumont Pliocene. It thrives on the deep alluvial arkosic sands of the California valleys. It grows on the dune sands of the California coast near Socorro and probably elsewhere (Fig. 6). There is a rare instance in Baja California of jojoba on heavy sandy clay derived from a porphyritic rock and subject to perennial polygonal cracking. Generally, jojoba soils are neutral to alkaline, have an abundance of phosphorus, and are subject to annual drying. This last appears to be a natural prerequisite, as it is generally lacking upon the bottomland soils of clay and silt throughout its range. Such sites are also colder than the adjacent slope lands.

Jojoba makes its best growth in areas having more than 12 inches of annual rain, as around the northern and western margins of the Sonoran Desert in

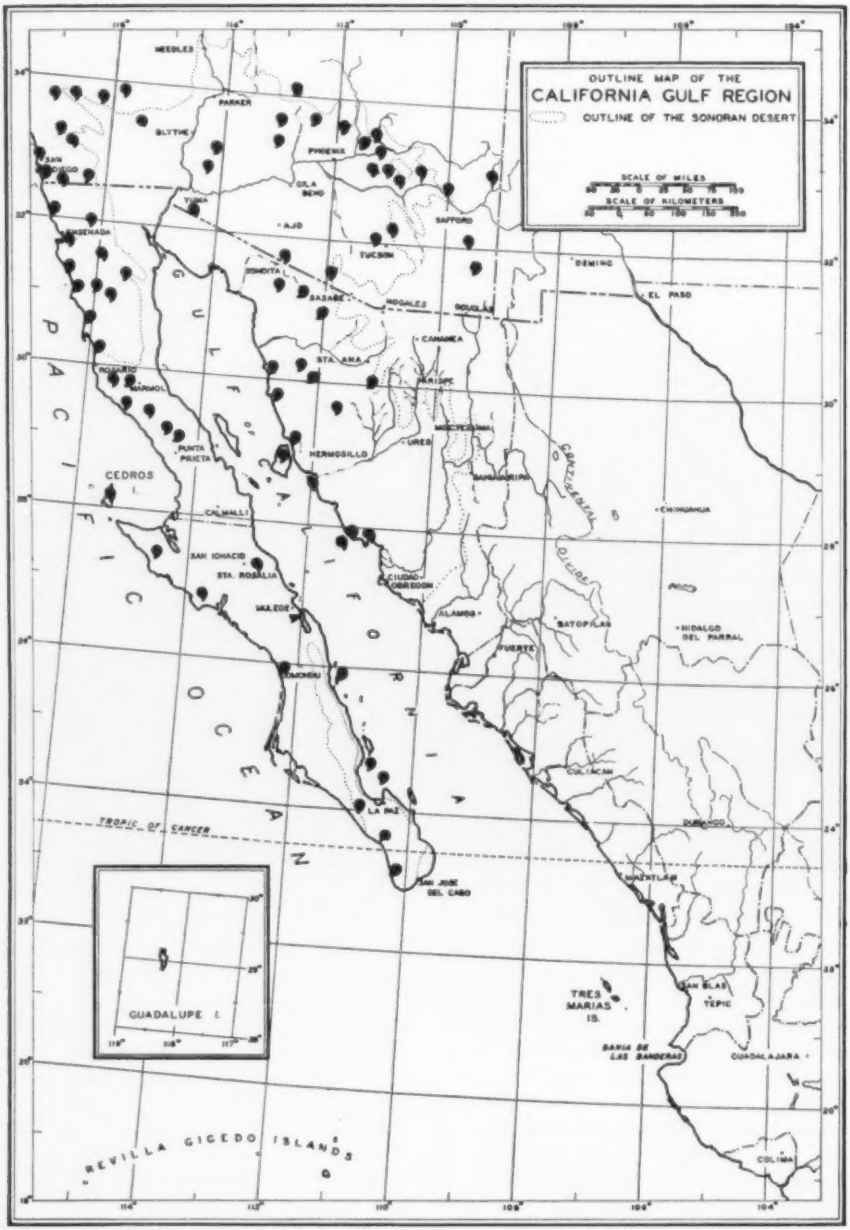

FIG. 3. The natural distribution of *Simmondsia chinensis*. Modified from Shreve (13).

central Arizona, southern California, and northern Baja California. Its area of greatest dominance occupies the slopes and valleys of the mountains north and east of Phoenix, where rainfall is 15 to 18 inches annually. Here it forms nearly pure stands over extensive rocky slopes (Fig. 7). Although it occurs in the desert proper, where rainfall is less than 5 inches annually, the plants appear limited there to sites having perennial run-off, as the sandy arroyo margins and alluvial fans at the mouths of canyons. Compare the dry nearly leafless aspect with a companion leafy plant along the pavement edge with run-off water in Joshua Tree National Monument (Fig. 8). Precipitation here averaged 4.3 inches annually during the preceding 10 years. The slow-falling, deep penetrating rains of winter and spring are much more important to its survival than are the hard quick convectional rains of summer which ordinarily moisten only the upper soil levels. Ten inches well distributed from October to April appears to be about minimal for general seeding.

Jojoba, living in the bright desert sun, is a true heliophyte and tolerates the extreme daily fluctuations of temperature which commonly range through 30 or 40 degrees during the morning. High daily extremes of 110° to 115° F., shade readings, are usual during the summer. Mature shrubs are known to tolerate temperatures as low as 15° F. without serious damage. Seedlings, however, are sensitive to light frosts of 3° or 4° below freezing and flowers are reported to be destroyed by late frosts although they are hardy in the bud. High sun temperatures on growing fruits cause sunburn and loss of seed (Fig. 9). The relatively

FIG. 4. The sandy clay hills near San Vicente, Baja California, with a natural cover of *Simmondsia chinensis, Eriogonum fasciculatum, Artemisia californica,* and others.

low winter temperatures synchronized with soil moisture build-up appear natural for jojoba reproduction.

The natural plant communities growing with jojoba provide further insight into environmental requirements. In the Arizona uplands of the Sonoran Desert (cf. Shreve, 13), its common arborescent associates are *Acacia greggii*, *Cercidium microphyllum*, *C. torreyanum*, *Olneya tesota*, *Canotia holocantha*, *Carnegiea gigantea*, *Condalia lycioides*, *Lycium andersonii*, *Yucca* and *Opuntia spp.* In northwestern Sonora these same species are joined locally by *Fouquieria splendens*, *Echinopterys eglandulosa*, *Jatropha cuneata*, *Atamisquea emarginata*, and others with *Yucca arizonica* replacing the more northern species of that genus. Along arroyos and on broad alluvial fans jojoba frequently grows closely with *Prosopis juliflora*, *Celtis pallida*, *Hyptis emoryi*, and other phreatophytes. However, it shuns the arroyo thickets of *Baccharis sarothroides* and *Tamarix pentandra*. It is also generally lacking in the dry, broad, open, extensive stands of *Larrea tridentata* and *Franseria deltoidea*.

In coastal southern California its associates form an open type of cover in the coastal sage brush association, typified by *Eriogonum fasciculatum*, *Artemisia californica*, *Salvia apiana*, *Rhus ovata*, *Lotus scoparius*, *Opuntia* spp., *Yucca schidigera*, and others. This same loose community continues into northern Baja California with *Rhus laurina*, *R. integrifolia*, and *Fraxinus dipetala* becoming conspicuous in frostless altitudes. On the coastal plains in a maritime community jojoba is one of the principal species with *Franseria chenopodifolia*, *Rosa minutifolia*, *Agave shawii*, *Aesculus*

FIG. 5. Jojoba on the coarse atrital soil near Yaqui Wells, southern California. The handkerchief and cap indicate the extent of the root system.

parryi, *Lycium* sp., *Bergerocactus emoryi*, and others (Fig. 2).

In the Californias, as in the Sonoran Desert, jojoba does not occur in the thicket cover of the broad arroyos, here formed by *Hymenoclea pentalepis* and *Pluchea sericea*. It is also excluded from Chaparral in both Arizona and California, although it may mingle with strays of the Chaparral species, as with

As with desert shrubs generally, the critical time for jojoba is during the seedling stage. Many years may pass without suitable conditions for germination and still fewer are the years when conditions follow on through to foster the tender seedlings. The natural conditions limiting the distribution, therefore, appear to be those unfavorable to ecesis. These negative factors are not

FIG. 6. A large fairy ring of jojoba formed by a male plant on the coastal sand dunes near Socorro, Baja California.

Penstemon antirrhinoides and *Rhamnus crocea*. Apparently, it cannot tolerate the closed communities occupying the more mature soils with higher rainfall. Its inability to compete in such cover excludes it from large adjacent areas which appear optimal for its growth and seed development. The Chaparral lands when cleared of competing brush, therefore, constitute a land class prospect for cultivation of jojoba; such are the dry-farmed grain lands of the Californias.

well understood for they could operate in any of the incipient stages involving seed burial, soil moisture and mineral nutrients, light effects on situations, temperature, plant-chewing predators, and so on. Were the seedling husbanded in cultivation, we could expect its establishment in an ecologic area greater than its natural one. It appears fit for cultural trials from central California to Florida on well-drained soils where winter lows only infrequently reach

15° F. The chances for successful cultivation are of course best within and adjacent to its natural area.

The Jojoba Fauna. A number of insects frequent jojoba. The more harmless include katydids, grasshoppers, darkling beetles, and leaf-chewing larvae. Wood borings have been found in old stems and a bostrychid beetle, *Amphicerus simplex* (Horn), hollows out twigs resulting in a random type of pruning (Fig. 10). A sap-sucking bug of the *Hemiptera* order was observed frequently among the leaves of the Aguanga jojoba. A microlepidopteron of the moth order is the only serious pest known. Its larvae chew out the young ovules and adjacent tissue in young fruits. The late Frederick Gibson and Baird (3) reported them as serious and during 1957 the writer estimates they destroyed about 75–80% of the fruit set in the Pinal Mountain region of Arizona. The geometrid moth, *Sterrha bonifata* (Hulst.), has been identified as a larva in stored seed of jojoba, but it is not known if this is the same moth attacking the growing ovules. The immature fruits with a perforation, where the insect emerges, are indicative of the latter pest. Chalcid flies have been observed to emerge from the fruits also. They apparently represent parasites of the moth and may constitute a natural check and a friend of the jojoba grower.

FIG. 7. An open cover of jojoba along the Apache Trail in the Pinal Mountains of Arizona.

Many rodents gather the jojoba nuts off the ground and some of them feed on the bushes, gathering the ripening nuts before they fall. Ground squirrels, *Citellus*, desert chipmunks, *Ammospermophilus*, and rabbits, *Lepus* and *Sylvilagus* spp., are among these. In most jojoba areas all of the nuts will be taken by animals, as in the Californias, where pack rats, *Neotoma*, are abundant. In other places, as near Superior and in the

Tucson Mountains of Arizona, previous year's nuts have been found lying on the ground. This condition was observed in the extensive stands where the seeds appear to be produced in excess of what the animal population consumed. Huey (9) has described a gopher, *Thomomys bottae jojobae*, which appears adapted to jojoba ecology. It is not known if it feeds on the roots. Deer and other browsing animals feed extensively on both fruits and foliage of jojoba (Fig. 11). The larger birds, such as jays, crows, pigeons, and doves have been reported to feed on or carry off the seeds.

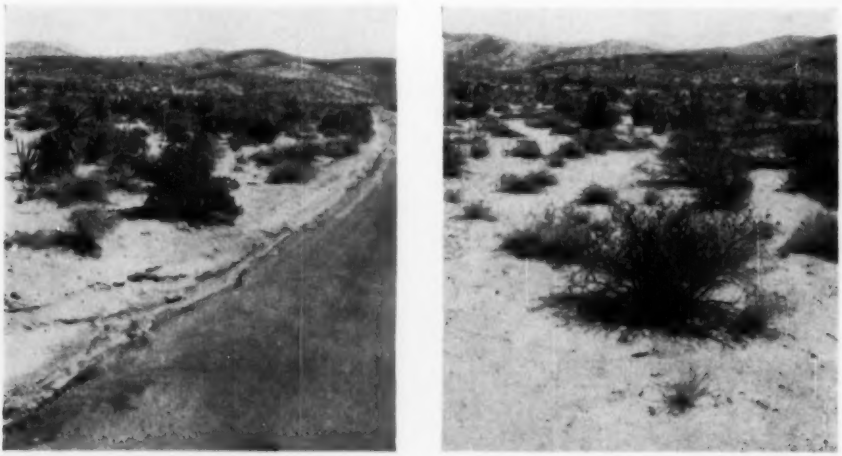

FIG. 8. A leafy growing plant watered by the run-off from pavement compared to a nearly leafless dormant plant away from the pavement. California Desert.

The Seasonal Cycle. The seasonal growth pattern of jojoba is generally a response to the winter-spring rains. Just when growth starts depends upon the amount and timing of the rains. With the flush of new shoots the flower buds appear in the axils of the leaves. The earliest that appear in fall or winter remain quiescent for three to five months until the warmer, longer days of late February or March. March appears to encompass most of the period of active pollination, but it may continue through April. When there are sufficient rains to provide deep soil moisture, shoot growth continues longer and is accompanied by a longer period of fruit setting. Light rains bring only a partial response from the jojoba population and the drought dormancy of many individual shrubs remains unbroken. Light rains fail to drive soil moisture to the deeper roots and those shrubs which have flushed a set of fruits frequently fail to mature seed, the capsules withering in the heat of summer. The seed crop of such years is light with small seeds low in oil and protein. Many shrubs, however, exhibit a self-thinning response, as there are frequently left some ovules that develop to seed. Fig. 12 shows the condition of growth and pistillate flowers on March 10, just previous to pistil extrusion and Fig. 13 of the same plant (No. 16376) on June 1, when capsules have attained their full size. The seeds or ovules, however, are still white and immature.

In 1957 jojoba did not seed well in

areas lacking fall rains, although spring precipitation was up to average in many parts, as Superior with *ca.* 9 inches and Aguanga with *ca.* 7 inches. Two distinct areas in Arizona and Baja California receiving 1 to 2 inches of rain in late November and early December were the only areas in which seeding was satisfactory although light. Also, in the dry Aguanga locality two plants having to have but little influence on the annual growth and productive cycle of jojoba. The late summer growth observed there was brief and ragged. B. W. Benson, of the Boyce Thompson Arboretum, Superior, Arizona, stated that there was but one definite growth period for jojoba; that of winter-spring. The summer rains, however, may fill out the maturing seeds and prolong their ripening.

FIG. 9. The withering green fruits show the effects of an early June sunburn. Aguanga, California.

heavy sets of capsules were not benefited by three irrigations of 50 gallons each during April, May, and June, as all capsules failed to mature seed on one bush (Fig. 9), while yield of the other developed about as did yields of other unwatered shrubs. Apparently, for maximum seed development, soil moisture must not only be provided deeply but early in the season or the fall.

The summer rains of Arizona appear This indicates that jojoba has its historical origins in the Mediterranean type of climate and the resting period imposed by the dry summer is normal to its constitution and perhaps essential to its health as some of the culture trials appear to indicate. At any rate, its growth cycle synchronizes naturally with the Californian climate, indicating that first cultural trials would be most likely to succeed there.

FIG. 10 (Above). Drying branches clipped by the bostrychid beetle borer. San Telmo valley, Baja California.

FIG. 11 (Below). A severely browsed bush showing how all twigs and foliage have been stripped in preceding years. Sierra Jojoba, Sonora.

The Variable Characters of Jojoba

Simmondsia is a monotypic genus with distinctive characters, and the only member of the Buxaceae except *Pachysandra* native to the United States. Once well-perceived, it is readily recognized wherever met. However, it is highly variable among individuals and populations in ways both obvious and obscure. Some of its variability is hereditary and some environmental, both sets of differences frequently being qualitative and not always separable when observed in nature. Mutations of large degree are obviously rare, the only striking instance observed being a single plant with three leaves at every node, growing in a laboratory at the Southern Utilization Research Branch in New Orleans.

Whether a shrub has single-seeded capsules or 2–3-seeded capsules may appear at first glance as a clear-cut distinction, only to be discarded as insignificant when both are found borne on a single shrub. However, when further study reveals that certain shrubs produce about 90% singles and another 80% doubles, a better evaluation of the character can be made. In *S. chinensis* nearly all phenotypes tend to grade into others, as though genetically we are dealing with multiple or cumulative factors. In wild populations the genetic lines have been repeatedly started and checked back again according to the fortuity inherent in a cross-breeding species. The general effect appears to have been the swamping out of potentially really distinguished genetic lines. Only in rare instances among geographically or environmentally peripheral populations, as in disjunctions, can we expect radical departure from the variant norm.

Taxonomically, the variants can be regarded as *forms*, but it does not appear desirable to burden the scene with formal trinomials at this time. There will be time enough for that as plant breeders select and stabilize the varietal lines of the cultivates. However, as many of the variants appear to have different potentials for jojoba as a cultivate, they are described below according to their gross morphology.

The Habit. Branching is profuse and the shrub generally forms with several to many stems from the root crown. In full light, characteristic of the normal site, lateral branching is prolific near the base. In a few years a symmetrical hemisphere of foliage arises from near the ground. As the plants age, gaining in height and breadth, shade pruning eliminates the early low foliage and a higher canopy develops. On old plants, dead, dry stumps and branches clutter the base area and there may be a deep litter of leaves and twigs. The strongest tendency towards plurality of stems may be evidenced as early as the first hypogeous shoots from seed, for two shoots may arise together from a single seed. Cutting of the initial shoot may result in branching at a lower node and a new basal shoot as well.

In the drier environments perennial growth is usually short and die-back common. This is reflected in short internodes and prolific lateral branching, forming through the years a very twiggy bush with dense, intricate branches. The wetter climates foster taller broomier shrubs of longer shoots with less lateral twigging. There are, of course, gradations between these environmental extremes of habit, but to orient the others keep these two in mind. Where long drought periods are interrupted by wet periods, the differential growth will be reflected in a distortion of habit. Where light winter rains are regular, a rather uniform population of low twiggy habit results, as in maritime California (Figs. 2, 4). Here the environmental control is rigid and masks the genotypes, which are evident as phenotypes elsewhere.

FIG. 12 (Above). Plant No. 16376 showing the flowers on March 10 just before pistil extrusion.
FIG. 13 (Below). The same shrub with full-sized but green immature fruits on June 1.

For instance, in the San Telmo valley 25 to 30 miles inland, the environment is quite different from its neighboring maritime one. The upper San Telmo valley with its deep sandy alluvium with both higher rainfall and temperature allows expression of many of the habit forms of jojoba: 1) the low twiggy form; 2) the tall broomy bush; 3) the long rakish branch form with an irregular open crown (rare); 4) the treelet form with loose or open foliage crown above a narrow base; 5) the thicket or clonal form consisting of what may appear to be individuals, which can be further divided into low, or tall, or open, or closed clonal forms, and so on.

When such habit forms occur at random within a given locality of uniform environment, it is apparent that such variants are largely genetic. In such a natural locus, however, certain factors may have operated to distort the present scene. One such factor appears to have been fire. Jojoba responds vigorously with new shoots following brush fires and it is probable that the thicket or clonal form is due to fire or some other form of top removal. On coastal sand dunes cloning appears as a response to sand burial. The tops of old plants continue to grow out of widely diverging points, appearing as individuals in a fairy ring (Fig. 6), while actually they are joined far below the surface in a single seminal origin. Regeneration after fire or cutting proceeds mainly about the root crown, but shoots also may develop several feet away like separate individuals from deep sections of the radiating main roots.

FIG. 14. Plant No. 16376 at Aguanga, California shows a symmetrical growth after burning by a brush fire. About 30 years old.

However, the different genetic endowments of these regenerated plants are attested by the respective forms they take, as the thicket clone, the broomy form, the twiggy form, and the rare single-

stemmed form. The latter is especially significant as indicating a constant genetic control of the individual through radically different conditions.

A habit difference between the sexes is usually apparent, the staminate plants being taller or larger with less die-back and knobbiness. They do not bear the onus of seeding. A good or heavy seeder may have a poor vegetative condition comparable biologically to the bony appearance of the good milker among cows. It is also notable and should prove valuable to the breeder that the staminate phenotypes have their habit counterparts in the pistillate forms. Some of the distinctive habits are shown in figures 2, 3, 14, 15, 16.

FIG. 15 (Left). Bush with open spreading habit. San Jacinto, Baja California.
FIG. 16 (Right). A large-fruited bush with erect open habit. San Jacinto, Baja California.

The Roots. Jojoba is a tap-rooted plant and the first response of the germinating seed is the deepest penetration possible according to soil medium and seed reserves. When cultured in deep pots the descending root is several inches long within a week and before the upward shoot has started. The root reaches depths of 12 to 18 inches by the time the shoot breaks cover. Each adult jojoba bush commonly has several tap roots developed by repeated forking below the crown. The maximum depths they reach are not known, but roots of many shrubs in different localities along eroded banks were observed from 8 to 12 feet below their crowns (Figs. 5, 17). The foreman of the Santa Marta farm in Baja California stated that the roots of one plant went to 10 m. depth in a well dug there.

No shallow or subsurface feeder roots or true rhizomes have been observed. Horizontal growth is never apparent except where subsurface strata prevent downward growth. Small down-trending laterals with "hairy" rootlets have been observed two to three feet below the surface. However, as the main roots at this depth were still large and little branched, it was apparent that most of the feeder roots are below that depth (Fig. 17). Wherever root systems have been observed, even at the lowest levels of eight or ten feet, the relative paucity of feeder rootlets is rather striking. A relatively vast volume of soil appears to be very poorly exploited by the jojoba root system. The need for a careful study of this organ is clearly apparent. Moisture and mineral intake should be

increased by stimulation of a larger feeder root deployment. The shallow adventitious roots obtained from cuttings might be the answer and it is regrettable that there are no field trials of such cuttings.

The Leaf. The leaf apparently lives through two or three seasons, depending on moisture and shade conditions. Eventually it develops an abscission layer on the very short petiole and falls. In 1957 there was a definite period of leaf-fall during the dry California summer. Older leaves are noticeably larger than those of the current year, indicating that growth continues during the second season. The soft green or gray of the first year passes to a paler yellow-green the second year. In age, the leaves are frequently tinged with reddish brown around the margin. Older leaves lose much of their initial fine pubescence and have a waxy indument. The blade is thick and rather stiff, standing divergently erect, but is easily detached if bent backwards along the twig, especially when young and tender and again when old and abscission is advanced.

The leaves on different plants vary in size, shape, color, thickness, and amount of pubescence. Some of these leaf forms are linked to or correlated with other characters, such as the small leaf and small-seeded capsule characterizing a recurrent form. When combined consistently with other definite characters, such leaf forms are significant in the recognition of the varieties or forms of *Simmondsia chinensis*.

A glaucous bloom appears on many shrubs lending a bluish gray cast to the foliage. Observers have regarded this as of varietal significance, but it appears to have no regular association with other characters and appears to be primarily physiologic. The new vigorous shoots from stumps of fire burn are conspicuously light glaucous gray. Its prevalence on a strong-shooted, vigorous, large-leaved form in the Santa Marta population suggests that it may be also an edaphic response. Like Kellogg's proposed species, *S. pabulosa*, based on an unusually pubescent form with small leaves, the light glaucous gray condition occurs at random through many populations. It may have significance as a leaf wax form. If so, the genes which control the glaucous character could become the obscure objective of geneticists.

Some shrubs appear to defoliate more readily than others and are relatively leafless at seeding time. This character when synchronized with fruiting time would have definite advantages for certain kinds of harvest operations. Leaf fall is concomitant with leaf aging and summer drought, but this does not explain why some shrubs at a given site will be nearly leafless, while others under the same apparent conditions remain in full leaf.

The Flowers. The female or pistillate flowers of jojoba are small and inconspicuous, being of the same pale green color as the new leaves and twigs (Fig. 12). They are borne in the axils of the leaves and the forks of the twigs concomitant with new shoot growth. Normally, only one of the two leaf axils at the node will flower in one season, the opposite bud remaining dormant. Capsules that frequently occur in the forks of twigs and rarely along leafless sections of the branches probably represent flower buds that remained dormant for two or three years. Both flower buds at alternate nodes may remain dormant during the first season resulting in flowering only at every other node. This is the general pattern in the Arizona populations, while the California plants commonly show flowering at every node in some degree.

Drought appears to be one of the strongest factors inhibiting the flower buds. When a season of good rains follows a long dry period these become activated along with those on the new shoot growth. Thus there is a sudden

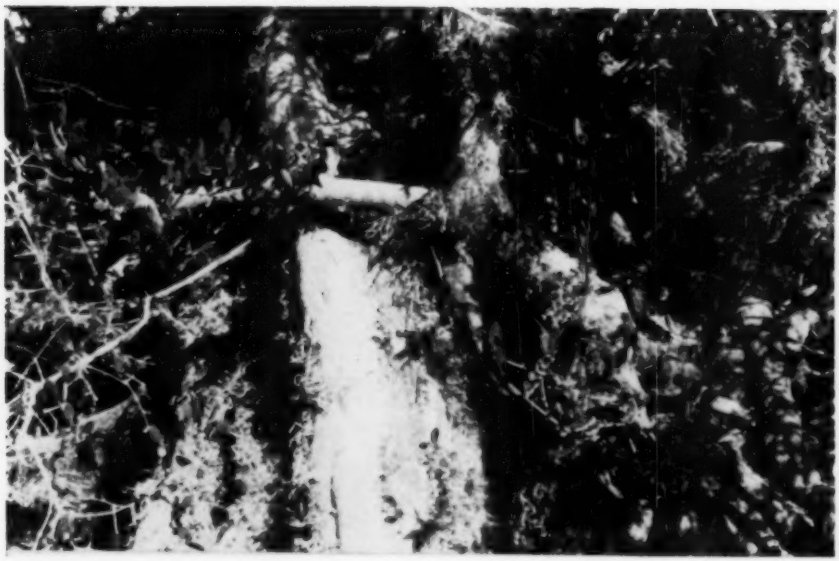

FIG. 17 (Above). A very old plant in the sand dunes near Socorro, Baja California. Wind has blown away the sand exposing the very large tap root and its branches.

FIG. 18 (Below). The same roots as above showing the epiphytic lichens and leaf shoots sprouted from the roots.

burst of flowers after two or three years of drought. Cold winter temperatures inhibit growth of flowers. This is demonstrated by the fall flowers which will winter over until spring, provided their pistils are not extruded before cold weather. The drought of summer and the cold of winter, therefore, tend to concentrate flowering in the spring. When soil moisture is present through spring and summer, as under irrigation, there is nearly continuous growth accompanied by flowering. This was the case with the Arlington planting. The result was lack of good correspondence between pollen and pistil. Seed maturation was also indeterminate and there was no harvest season as normally prevails among wild populations, synchronized with the natural season.

The clusters of small yellow male flowers are also borne in the leaf axils and follow the same regime as the females. In natural jojoba populations both sexes appear to be well synchronized to moisture and temperature and there is usually abundant pollen for receptive pistils in the spring. The pollen is borne easily by the wind and fruiting pistillate plants have been observed a half mile or more from staminate bushes, indicating that pollen is borne such distances. No insects have been observed on the female flowers, which are "colorless" and without nectaries or scent glands. Some individual plants of both sexes, however, flower early and others flower a month or more later. At Santo Tomas and San Vicente, some female flowers failed to set seed in 1957, apparently for lack of pollination. Conceivably in domestication, the selection of a late-flowering female variety could impose a corresponding selection of a late pollinator, but it now appears as a remote problem.

The ratio of male plants to female plants in Arizona is very unequal. Gibson and Benson of the Boyce Thompson Southwestern Arboretum reported to the writer that the jojoba population at Superior had about five males to one female and counts were subsequently made at that and other localities, as follows:

	Males	Females
Superior, Arizona ..	100	23
Tucson, Arizona ...	80	40
Camp Creek, Arizona	3 or 4 to	1 (estimated)
Aguitos, Baja California	31	20
Meling Ranch, Baja California	77	62
San Telmo Valley, Baja California ..	50	50
Aguanga, California	30	27

The cause of the disparity in the sexual ratio in Arizona is not certainly known, but it appears to be due to environmental rather than genetic factors. Apparently, three to five males will survive the stresses of seedling establishment where as many females will fail.

There is another conspicuous difference between the Arizona and the California

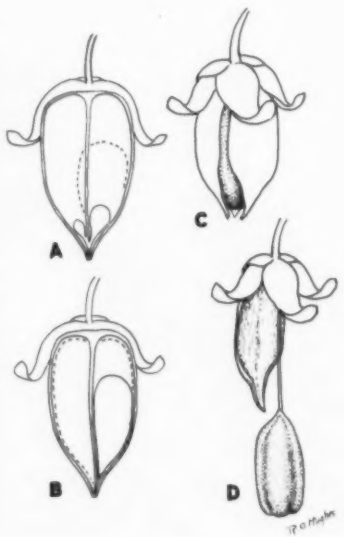

FIG. 19. Development of the ovule; A, at three weeks; B, at eight weeks; C, at seven months dehiscence; D, the hanging seed.

populations. Flowering at every node is very common in the Californias, but relatively rare in Arizona. This appears to have a genetic basis because Arizona seeds growing at the Huntington Botanical Gardens and at Vista in California retain their habit of flowering and seeding at alternate nodes. Arizona stocks would appear to have less yield potential than the California stocks. Further genetic deployment is shown by the polycarpy of Fig. 19. The evolution has been from alternate to nodal to fascicled and racemose or vice versa (Fig. 20). Fasciculation occurs in varying degrees with the individual shrubs having the trait in some percentage of the total peduncles, as 10 or 20 or 60% of the peduncles with fascicled fruits and so on. What is involved here by the mechanics of growth and physiology in conjunction with the genetic mechanism is not understood. Its applied significance is discussed below.

The Capsules. The individuality of jojoba is expressed more fully in its fruits than in any other organ. The fruit is a capsule (Fig. 19a), normally dehiscent, containing one to three ovules attached to the placenta at the apex of the capsule. The ovule, therefore, grows from the apex towards the base of the capsule in an upside down position. The capsule attains nearly full size in about three months. It grows more rapidly than the ovule and within five or six weeks forms a relatively large cavity, which the growing ovule or ovules will gradually occupy (Fig. 19). During the early stage, the first two to three months, the ovule is a soft creamy-white ovoid to pyriform body. If seasonal conditions are unfavorable for development, it may wither before filling the cavity. Under good conditions the ovule will completely fill the cavity, molding itself to the form and in time, as it matures to a well-filled seed, may assist in splitting apart the three drying valves of the capsule. The period required for complete maturation after fertilization is six to seven months. Seeds that matured prematurely in five months were found to be viable, but small, withered and low in oil content.

The factors determining whether one, two, or three ovules develop are unknown. Ovules may be found in all stages of abortion. Shrubs which usually develop 2-seeded capsules commonly have one seed much smaller than the other. One-seeded, 2-seeded, and 3-seeded capsules occur on some individual bushes. However, individual shrubs tend to have a high percentage of one or the other, some having 80–90% one-seeded capsules and so on. There appears to be a primary genetic control modified by environmental conditions.

The capsules vary notably in size, shape, and color (Fig. 21). It is apparent that each triad differs from any other triad, while the members of each triad show their likeness. This reflects the genetic character of each shrub the triad represents. They may be relatively short and round, long and pointed, large or small, ovate or elliptic in outline, somewhat bell-shaped or obovoid being broadest just beyond the middle. Their respective shapes are partly modified by the number of seeds, the 2–3-seeded forms usually being fuller and shorter than 1-seeded forms. However, the effect of seed number on capsule form appears to be secondary to a genetically determined capsule form, as individual shrubs have recognizable capsule shapes, irrespective of the number of seeds they contain. For instance, the form with short round capsules will maintain this form irrespective of the number of seeds in different capsules on the same bush. The 3-seeded capsule will usually be larger than its companion 1-seeded capsule, but the capsule form is otherwise the same. As another example, the long capsule form may have a high percent-

FIG. 19a. Capsules of jojoba showing single and double-seeded fruits found on one cutting. Aguanga, California, 1952. (Photo. natural size.)

age of obovate capsules due to the presence of 2 seeds, one of which is smaller and has filled out only the lower or more distal part of the capsule. It is not always possible to tell by the exterior form of a capsule whether it contains one or more seeds. This is true of several forms making up the common medium ovoid capsule types.

Some of the capsule forms appear to be correlated with certain leaf forms, as small capsules with small leaves, large, thick-walled capsules with large thick leaves, and long capsules with long leaves. This suggests that growth factors operate on leaf and capsule alike. The genetic basis of such forms is further evident by their random occurrence within certain populations and again others which recur as recognizable types in several populations. A shrub form, characterized by small-seeded, small capsules, long-pubescent capsules, and small leaves, has been observed in the

FIG. 20. The evolution of fruiting in jojoba: A, typical; B, nodal; C, fascicled; D, racemose.

San Vicente, Santo Tomas, and Aguanga localities of the Californias.

The tendency toward clustered or fascicled fruits is of unusual interest. It is rare among jojoba fruit forms and suggests definite advantages for high potential yields and for hand picking. Stunted shrubs or dwarf types with very short internodes of one-quarter inch or less may give the appearance of having double or triple fruits, but truly fascicled capsules are borne on a single peduncle (Fig. 19). All characters in jojoba differ gradually or by degrees and this is especially evident in fascicled fruiting. In most localities it occurs as a small percentage (one to two percent) of double or triple capsules on a very small percentage of the shrubs. In other localities, notably at Santo Tomas in northern Baja California, shrubs with fascicled fruits make up 10 to 15 percent of the female population. Some of this percentage is composed of individual shrubs with 25 to 40 percent of their peduncles having two to six capsules each. In such a locality as this, it would appear that factors for this character hold uncommon sway and the plant breeder could gain by using the local germ plasm for studying this character.

The growth form of the racemose inflorescence is itself variable. It does not appear to be linked to any one capsule form, as round or long, 1-seeded or 2-seeded, and large or small capsules have been found in one inflorescence. The fruits are commonly short-pedicled and inclined to bunch together. Very rarely has a long-peduncled, loosely composed, freely hanging, racemose cluster been observed (Fig. 20). The long peduncle, allowing the growing capsule to hang down, shaded by the leaves and the calyx lobes, is a valuable situation, since it prevents the high sun from striking the young tender capsule. The short-peduncled capsules and the short-clustered fruits in particular were the types that suffered most from sunburn in the early June hot spell of 1957.

It would appear that fascicled fruiting is potentially a very valuable character, as two or three or even six seeds could be produced where only one commonly grows. The case, however, is not so simple. In addition to the sunburn drawback mentioned above, fascicled fruits growing on wild shrubs have smaller seeds, many of which fail to mature. Generally during the unfavorable seeding year of 1957 the more capsules this form had, the fewer were the mature seeds. At Aguanga, where moisture conditions were poor during 1957, none of the fascicled-fruited shrubs under observation were able to mature seed. The fruits either sunburned and shriveled away or shriveled away without being sunburned. Hence the successful cultivation of this outstanding form will depend upon our ability to meet its more critical requirements for seed maturation. It is not to be recommended for dry-farmed lands, but irrigation, fertilization, and other cultural advantages may eventually justify the selection of improved varieties of this form.

The Seeds. The large peanut-sized seeds of jojoba contain little or no endosperm and consist mainly of the undifferentiated tissue of the cotyledons. At hypogeous germination these become swollen with moisture into large succulent subterranean organs, carrying large reserves of energy for the young plant. As the seed matures the seed coat darkens, becoming light reddish brown before the green capsule opens. By full maturity the seeds are commonly brown, but seed color varies according to individual shrubs and populations, a chestnut color being common at Camp Creek, while chocolate brown is usual about Superior. The seeds on different shrubs also vary in size, shape, amount of pubescence and its distribution, lumpiness, etc. (Fig. 22).

Seeds borne on different shrubs have

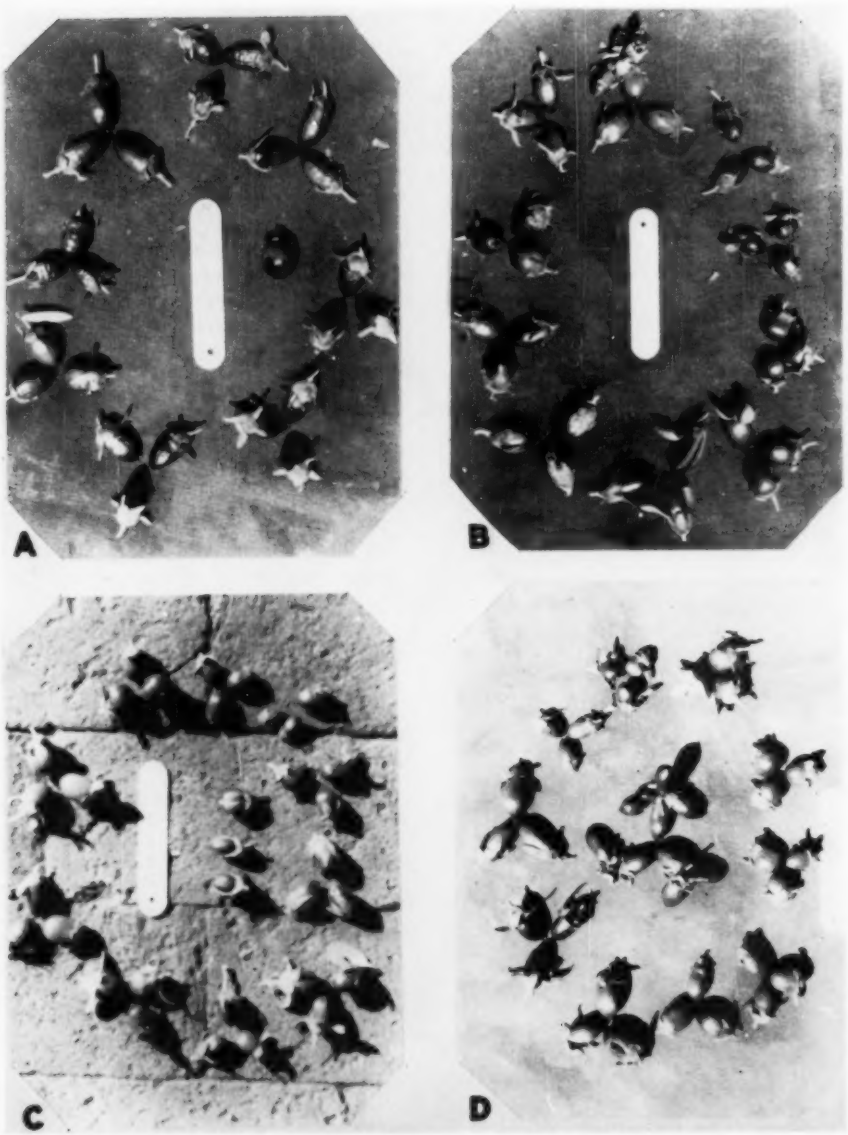

FIG. 21. The variable capsules of jojoba; each triad represents a single shrub. A, Superior, Arizona; B, Camp Creek, Arizona; C, Aguanga, California; D, San Telmo Valley, Baja California.

been found to vary in size from 336 to 2335 per lb. This is a sixfold difference, suggestive of what might be done with this variable character in a few generations by selective breeding. Large well-filled seeds have many advantages from the harvest and yield standpoint. There are many factors involved. There appears to be a basic genetic mechanism for seed size, as individual shrubs have their respective seed forms. Other determinants of seed size are whether there is a large or light set of capsules (generally the fewer the capsules per bush, the larger the seeds), and upon such seasonal conditions as deep soil moisture, etc., and which are discussed later (p. 287).

The seed appears to draw nutriment from the capsule as long as the capsule remains green and functional. Capsule and seed mature together and under proper conditions the drying capsule splits open along the three sutures, the valves falling away from the calyx with any agitation of the bush, as by wind or animals. During the time of seed fall, one can observe seeds and valves in all stages of gradual fall. Frequently, the seed may be seen hanging down from the calyx on its slender placenta, as on a string, Fig. 19 D and will fall at a touch when the placenta has dried. With proper dehiscence the seed falls free upon the ground among the litter of leaves, twigs, calyces and valves. When capsules dry prematurely they shrink and may fail to open. If this occurs late enough, the seeds may be viable or otherwise usable, but it is then necessary to crack and shell the capsules. By hand methods shelling is done by tramping to break away the thin capsules followed by winnowing. Such dry withered capsules are apt to remain on the calyx and bush for a considerable period.

The season of seed fall is predetermined by both environmental and genetic factors. The season will be late and prolonged according to the moisture and coolness of the spring and summer, or early according to the dryness and heat of those seasons. These factors in wild populations appear to over-shadow the effects of an early or late blooming period. However, the genetic factors are apparent in the difference of seed maturation according to individual shrubs inhabiting the same locality. Some shrubs ripen seed earlier or more determinately than others. Generally the seed fall will continue over a period of six or seven weeks in a given locality, some shrubs seeding throughout this period while others will complete the process within a month. Usually the southern populations in Baja California will mature seed one or two months earlier than in California or Arizona, but there are seasonal exceptions. In 1957 seeding was unusually early and short in Arizona, from middle July to late August, while it was latest at Aguanga in California, where general ripening did not occur until mid-September. It appears that man can improve the seeding habit for harvest purposes by selecting determinate-seeding forms and by proper irrigation timing, but there is little he can do about the vagaries of climate.

Yield of Jojoba

The potential yield of jojoba has been a crucial question in appraising its economic position. Previous estimates have had no quantitative data available (5). Part of the field survey of jojoba during 1957 was directed towards collecting yield data from cultivated jojoba and from wild shrubs. The individual seed yields of 80 wild shrubs were collected and weighed separately. The lots varied from two ounces to six pounds per bush or clone and averaged 1.5 pounds each. Such bushes represented only a small percentage, about 5 to 25%, of the female populations, as most of the shrubs did not yield during 1957. Years when

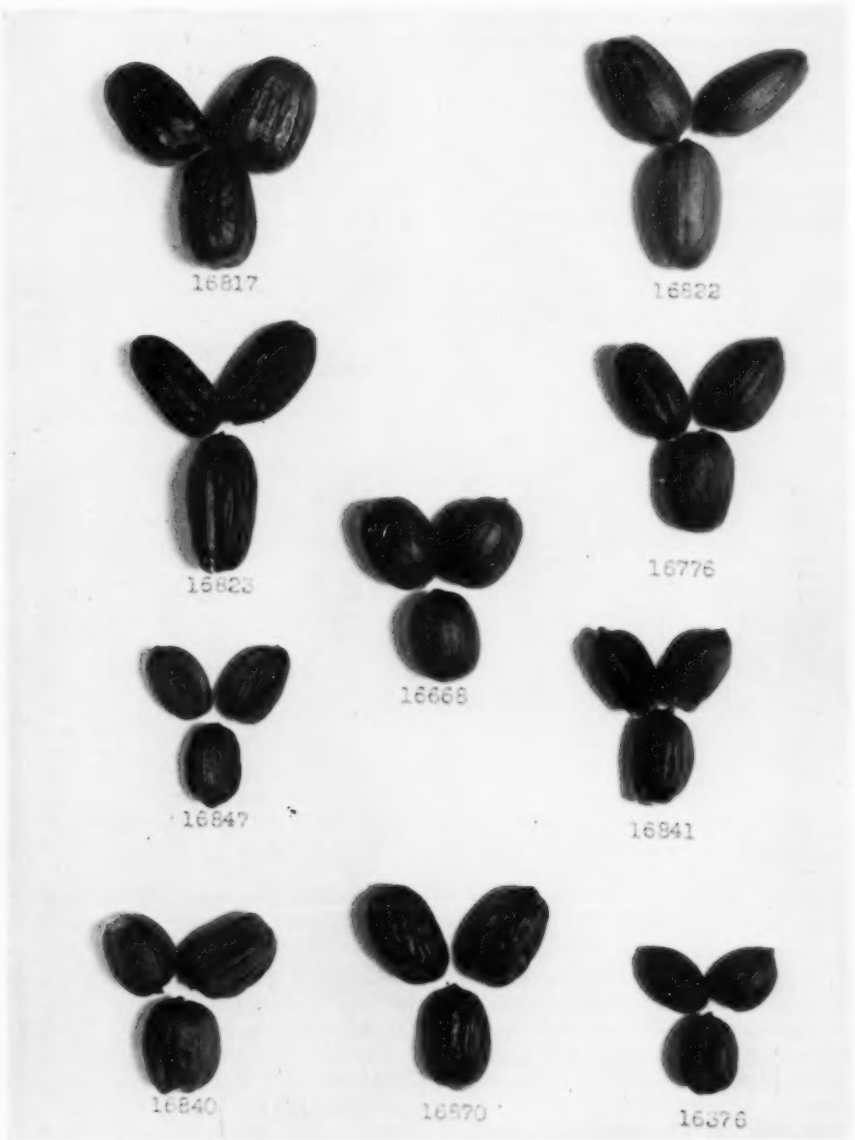

FIG. 22. Seed of jojoba, natural size. Each triad represents an individual shrub: 16817, 16822, & 16823 from Camp Creek, Arizona; 16776, 16847, 16841 & 16840 from Baja California; 16870 & 16376 from California. No. 16668 from a cultivated plant at Huntington Botanical Gardens, California; note the full smooth roundness of this cultivated seed.

fruiting was more abundant and general among jojoba stands have been reported by local residents and observed by the writer. In such seasons, one in every five or six years, seed production of individual shrubs and of localities as a whole is higher. Seeds of twenty of the eighty shrubs, collected to obtain their individual oil contents, are reported in Table 1. These represent the higher yielding shrubs and have an average of 2.5 lbs. per bush or clone. The wild crop of jojoba seed will, therefore, vary greatly from year to year, for any given locality or area.

Previous analyses, based on composite samples of Arizona seed, show an average oil content of 48 to 50% (5, 6, 7). Table 1 lists the oil content of 26 individual shrubs or clones analyzed by the Southern Utilization Research and Development Division of the U. S. Department of Agriculture at New Orleans. With a difference of 16 between the low instance of 37.8% and the high of 54%, they show a spread of over 30% variation in oil content among individual plants. This is large enough to command more attention.

TABLE 1

YIELDS OF INDIVIDUAL WILD SHRUBS OR CLONES OF JOJOBA. THE OIL ANALYSES WERE MADE BY THE SOUTHERN UTILIZATION RESEARCH AND DEVELOPMENT DIVISION OF THE U. S. DEPARTMENT OF AGRICULTURE IN NEW ORLEANS

Plant No.	Locality	Yield in lbs.	Seed size	% oil content	Date
16799	Superior, Arizona	.75	1040/lb.	47.1	July 1957
16801	" "	1.5	760/lb.	45.8	" "
16803	" "	.5		42.8	" "
16808	" "	1.5	480/lb.	48.3	" "
16818	Camp Creek, Arizona	1.	500/lb.	47.2	Aug. "
16820	" " "	2.	480/lb.	45.4	" "
16829	" " "	.5	775/lb.	44.9	" "
16748	Santo Tomas, Baja Calif.	2.5	540/lb.	44.2	Aug. "
16874	" " " "	.75		40.6	July "
16776	San Vicente, " "	1.3	640/lb.	49.7	Aug. "
16777	" " " "	2.	825/lb.	51.6	" "
16779	" " " "	2.	950/lb.	44.0	" "
16780	" " " "	1.2	1280/lb.	48.6	" "
16843	" " " "	1.	2335/lb.	37.8	" "
16773	San Telmo, " "	2.5	775/lb.	47.8	" "
16838	" " " "	5.	950/lb.	44.0	" "
16839	" " " "	4.	1000/lb.	45.6	" "
14262	" " " "			44.0	Aug. 1949
16862	Calentura " "	5.7	1000/lb.	47.2	Aug. 1957
16376	Aguanga, California	6.	1500/lb.	42.3	Sept. 1957
16852	" "	3.5		45.0	" "
14240	" "			45.6	July 1954
14266	" "			53.0	Sept. 1954
14267	" "			51.3	" "
14268	" "			54.0	" "
14272	" "			51.2	" "
16668	Hunt. Bot. Gard. "	65.*	575/lb.	50.1	Oct. 1956

* Estimated yield of two cultivated shrubs growing together.

The generally lower oil content of the 1957 seed samples, averaging 45.6%, compared to the average of 51% for 1954 appears to reflect the poor seasonal conditions for seed maturation which prevailed during 1957. This is to be expected on physiological grounds. It was expected in 1954, when individual shrub sampling was initiated, that analytic values would lead to the selection of individuals with high oil content. While

the data obtained indicate some inherent individual differences, it is not possible to evaluate them properly because they are masked by the deterrent of immaturity. There are too many environmental factors detracting from the plant potential. To eliminate these prejudicial factors, it will be necessary to run several test series: 1) a series of samples from several shrubs taken at various stages of seed maturation; 2) another series of wild shrub samples during a season favorable for seed maturation, all taken at their respective times of seed fall; 3) a series of samples from individual plants cultivated under uniform conditions. The full potential of oil synthesis by the plant can eventually be determined when culture and nutrient feeding systems are tried and developed for building high oil content.

Among the many factors contributing to the lightness, or diminution, or failures of the 1957 seed crop, the following appear important: (1) insufficient deep soil moisture; (2) failure of shrubs to break dormancy; (3) failure of flower maturation; (4) sunburn of green capsules; (5) moth infestation; (6) rodent and bird depredations. These factors operated variously in different localities or regions. Lack of deep soil moisture was a general condition, due to the many preceding years of subnormal rainfall, and apparently accounts also for the lack of flower response in many shrubs. At Aguanga, many shrubs responded to a heavy January rain with a prolific burst of flowers and good sets of fruit lasted on into May. They appeared to have fine seeding prospects at that time, but following an early hot spell the first of June there was extensive damage and continuing failure of the fruit set through the summer. Moth damage was very severe in the Pinal Mountain region of Arizona, where it was estimated that about 75% of the young capsules were eliminated by this pest. Birds and mammals do not directly contribute to the failure of fruits to mature, but they do take a percentage of the potential harvest before pickers can get to the shrubs. Rabbits clip those within their reach, while squirrels, packrats, and mice climb the bushes to gather the ripening nuts. Where cattle range, they may browse the bushes severely and prevent any general development of fruit (Fig. 11). This was the general case through northern Sonora during 1957. Altogether, the reproductive function of jojoba suffers many adversities.

Quantitative yield data from cultivated jojoba are very meagre:

Coit planting, Vista, California—0.5 lb. per plant, 5th year.
Huntington Botanical Garden, Calif.—5.0 lb. per plant, 12th–15th year.
Huntington Botanical Garden, Calif.—32.5 lb. per plant, 22nd–25th year.
Univ. Arizona farm, Arizona—"handful" in 16 years.

The Huntington Botanical Garden appears to be the only source of data for any series of years. Mr. William Hertrick, retired superintendent of these gardens, reported about five pounds per annum for three plants between ten and fifteen years of age during the mid-forties (letter to Fred Gibson). Two of these shrubs are represented in Table 1 by No. 16668, which are reported to have yielded over 30 pounds each in 1956, when the shrubs were 22–24 years old. These two shrubs were cultivated in the succulent garden with about two light sprinkler irrigations annually and were kept well pruned to avoid tall tops. On the basis of yield records of wild plants, this report appeared incredible, and a special trip was made to the Huntington Gardens to investigate. Unfortunately, these two shrubs had been eliminated and they could not be examined, but conversations with the gardener, Mr. Joseph Schneider, who picked the 1956 yield, substantiated the yield

report. He had weighed one gallon bucket of seed and then multiplied by the total number of buckets picked. If we accept his figures as a possible potential yield of cultivated jojoba, we can re-examine what may be inferred from experience with wild shrubs.

For this purpose, shrub No. 16376, a thirty-year-old dense bush (Fig. 14), was under close observation during the 1957 season. It bore a prolific set of flowers during March and in connection with a pollination test total flowers were estimated to be about 20,000. When picked in mid-September the seeds weighed 6 lbs. with 1500 seeds per lb. About 10% of the capsules bore double seeds, the rest were singles. Less than 9000 flowers were represented in the weighed yield. Over 10,000 or more than half of the original set of flowers, either failed to set and develop or the seeds were carried off by birds and rodents; activity of the latter was clearly apparent at picking time. The small seed size appears partly due to the poor moisture conditions prevailing during the 1957 season. Assuming that seed size could be doubled under proper culture, or enlarged to 750 seeds per pound, and the 20,000 flowers brought to maturity as seed, there would be a maximum potential yield of 26.6 lbs. A larger-seeded shrub (500/lb.) would convert 20,000 flowers into 40 lbs. From this line of reasoning, the Huntington report does not seem incredible. However, such a yield is not to be expected every year, and is scarcely to be entertained for predicting field yields. As a theoretical maximum, it can be regarded as an objective for future breeders and agronomists of jojoba. If they can do for seed what the Arlington planting did for vegetative response, it should be easy. At present I can find no quarrel with previous estimates indicating about 1 ton of seed per cultivated acre (5), but this could not be expected until after the tenth year. The Huntington report makes this estimate appear conservative.

Wild jojoba represents a rich source of materials basic to any research that may be conceived or activated for the plant. Its wide ranging variability is only outlined in the preceding discussion. Not all its variables can be perceived or judged by periodic observation under natural conditions. There are too many environmental effects. For instance, individual shrubs which appear as heavy seeders at one season, may fail to yield the following year, or a vigorous individual may owe its performance to a favorable local site rather than to inherent factors for vigor. However, some of the intangible factors can be evaluated by repeated observations over a period of years. The study of individual wild shrubs is of importance as research economy in view of the long generation period of five to six years. Two or three years of consecutive study of wild populations should save, by the location of desirable prototypes, many years of selection through cultivated progeny of unknown origin.

However, field selections could never compete with selections that would develop with cultivated lines. Only under the more uniform conditions of culture can the successful cultivated strains materialize. The respective adaptabilities of plants or varieties are demonstrated only when the subjects are placed in the environment of cultivation. The plasticity of plant species is an individual thing, and it has been well demonstrated that certain individuals will survive where others will fail (6). The initial start of an agronomic program, however, will depend in large measure on the adequacy of the original planting stock.

On the whole it appears that many potentially valuable varieties or strains can eventually be selected. The kinds to be maintained will depend upon the environment or region they will occupy,

upon the methods of cultivation and harvest, and upon the kind of product itself (just seed or seed plus leaf). Some of the jojoba variants can be suggested as more desirable for certain purposes at this time:

1) The erect, single-stemmed, low, even-crowned bush would lend itself well to cultivation and to harvest.

2) The many-stemmed coppice or thicket form might be desirable for harvest by mowing.

3) A form that sheds its leaves before seed maturity would facilitate picking.

4) Determinate seeding would concentrate seeding in a short period and make harvest operations less expensive.

5) Freely flowering forms would provide culture methods with a better potential for increasing yield.

6) Late flowering forms would avoid frost damage to flowers.

7) Larger seed size and higher oil content would increase yield according to seed unit.

8) Fruiting at every node theoretically would double that of alternate nodes and the nodal strains should have preference for cultivation with irrigation and fertilization.

9) Fascicled fruiting would greatly favor hand picking and possibly increase yield above average.

10) Long-peduncled fruits would minimize sunburn damage.

The factors determining the characters of these forms appear to be primarily genetic. The stabilization or building of such forms, as well as the development of others not yet perceived, is for the geneticist. However, he will need to know the types of plants best suited to cultivation and harvest. In this he will need the guidance of the agronomist and engineer.

Jojoba as a Cultivate

I examined a number of experimental plantings in 1957. These were the irrigated Eddy planting near Riverside, California (Fig. 23), the dry-farmed Coit planting near Vista, California (Fig. 24), and the University of Arizona test plot at Tucson. I have also had the Eddy planting under observation intermittently since 1947 and during these years have made several culture tests of the plant on my farm near Murrieta, California. The following discussion of culture methods and ideas is a brief perspective of these experiences.

Propagation. Unlike most oil seeds, jojoba seeds retain their viability for several years. A recent test to determine viability of 11-year-old seeds, stored in an open shed in California, gave 38% germination compared with 99% and 98% germination for 6-month-old and 2-year-old seeds respectively. Storage with controlled temperature and relative humidity conditions would doubtless greatly prolong longevity. Immature seeds may also germinate readily. However, as the young seedlings are fragile in many ways, it is important that they be started with robust, well-matured seeds. They germinate readily in alkaline sandy media if kept moist when daily temperatures range from 80 to 100 degrees F. They have responded less well in tests made in acid media. In California both field and outdoor nursery seedlings have responded well from March to October. Fall seedings have been inhibited by low temperatures resulting in spotty germination with lower vitality in the spring seedlings. If seedlings are to be set out in regions where frosts occur, it is advisable to start them in the spring and harden them off by drying as much as possible before winter frost.

The seeds should be pressed firmly in the substratum 1 to 2 inches below the surface, particularly when topped with sand or vermiculite mixtures, as the powerful thick radicle may otherwise push

the seed above the surface, where it drys. Crusting soils should be kept moist until after shoot emergence. Out of doors the top shoot will appear in three to four weeks, somewhat sooner in greenhouses.

Jojoba does not transplant well. Several trials have resulted in the loss of the great majority of plants. Root pruning or other techniques may be developed to correct this (4). Potted plants when moved to the field have also shown definite shock or set-back with several months to a year required for recovery and resumption of growth. This appears due to injury to the tap root, which penetrates deeply within a few weeks. Studies of transplant handling are badly needed.

Jojoba may either be direct-seeded in the field or transplanted from potted nursery stock. There are respective advantages, depending upon local circumstances. Field seeding has been done economically with a modified cotton planter. In direct seeding it is best to apply two or three irrigations after germination through the first summer and the seedlings should be protected from rodents, birds, and insects. Weeding should follow each irrigation. Potting can be handled successfully in tar paper pots of medium to heavy grade and should be at least 12 to 15 inches deep to allow root room. When set out in the field, the paper cylinder can be raised several inches to provide protection from frosts and rodents. It may also serve to reduce bushy branching from the base and start the seedling on a treelet form. There are several drawbacks to this method, however. One is cost, another is set-back due to root injury in moving and even loss of some plants. A continuing problem is the heating developed within the cylinder

FIG. 23. The Eddy planting near Riverside, California, at about six or seven years of age with irrigation.

around the tender seedling during hot summer months. Painting the cylinders white on the sun-side should eliminate the excessive heat, however. The advantages of nursery-started seedlings are obviously those of controlled conditions best suited to their early critical period. As their growth is slow it may be advantageous to hold them in pots over two winters when they would be

FIG. 24. The Coit planting near Vista, California, in the fifth year (1957), dryfarmed. Carob bean orchard in background.

hardier and it would theoretically shorten their unproductive period on the land. There is little evidence available at this time for evaluating these suggested methods and the need for further research is quite obvious.

Cuttings of jojoba have been rooted. In several cases reviewed by the writer, it was found that only new shoot growth treated with root promoting substances, as indoleacetic acid, responded well. Adventitious roots were formed on 50% to 80% of the cuttings tried. However, in no case were such cuttings continued beyond a few weeks, so it is quite unknown whether such propagations will produce successful mature shrubs. The advantages of vegetative cuttings in multiplying desirable selections are obvious. Also, an adventitious root system might prove very desirable in improving the general root efficiency of jojoba. It would appear much more capable of absorbing the soil moisture and minerals from upper soil levels than the very deep tap-rooted plants grown from seed. Such propagation studies, therefore, should be carried through to the final maturation of the plants and even better to the effects of nutrient feeding on yield.

Field Practices. Irrigation after the first two summers, when the critical period of seedling establishment is passed,

should be practiced with restraint. This is strongly indicated by several lines of evidence. The Eddy planting demonstrated the effects of prolonged irrigation resulting in excessive vegetative growth with unseasonal and feeble seeding and ultimately in the death of most of the shrubs in their eleventh year. As far as can be learned, this planting was irrigated about once a month during spring and summer from early May until fall, along with orange trees. The Coit dry-farmed planting, on the other hand, has progressed more slowly but surely with normal seasonal seeding starting in the fifth year with light rain years of eight to ten inches. This indicates that irrigation if needed should be applied synchronously with the growth and seeding habit of jojoba. It appears that one fall irrigation heavy enough to supply deep soil moisture and another in late spring would not unbalance the natural regime and would guarantee the deep soil moisture required for developing ample root systems and adequate yields of mature shrubs. As indicated above, deep soil moisture deficiency appears to be the leading factor accounting for seed failure in wild plants.

Spacing. Spacing should be commensurate with the first full bearing decade, from 10 to 20 years, for this should be the period when capital and profit return. The Eddy planting with a maximum growth rate filled a 10×10 foot spacing in 10 years. A 6×12–14 foot spacing would allow room for row culture and provide more plants per acre, 576 to 500, and should be adequate for dry-farmed methods. If more space is desired after 18 to 20 years, every other plant in the row could be removed. Inter-cropping could be practiced during the first six to eight years, preferably with such crops as winter peas, chick peas, Egyptian clover, or other nitrogen fixers suitable to the winter-spring growing season.

On slopes, like much of the dry-farmed grain lands of southern California, the rows should be contoured or terraced. This would probably mean fewer plants per acre, but the preservation of soil and moisture is of first importance.

The pollination experiment conducted at Aguanga during the spring of 1957 established the fact that pollen is essential to seed development. No fruit developed in flowers bagged just previous to pistil receptivity. Male pollinating shrubs will, therefore, be necessary in plantings. Fifty pollinating shrubs per acre has been suggested (5). This number appears to be adequate, as pollen is produced abundantly, carried widely by the wind, and pollen time synchronizes well with normal spring flowering. The pollinators should be spaced according to prevailing wind currents at flowering time. In the California coastal region this would be the seaward side of the planting, for the on-shore westerlies would then carry the pollen over the pistillate shrubs. Where conditions are ideal, the number of pollinators needed would be less. In any case, an outside hedge of males around a field of females would have many advantages. Pollen would then be available from any windward quarter, the tall more robust males would act as protecting wind breaks, and in general they would be out of the way of harvest operations. As with all other aspects of jojoba, however, many problems can be expected to arrive concerning the kinds, the numbers required, the spacing, and the effects of individual pollinators.

Pruning. Jojoba responds readily to pruning and shows growth improvement in both wild and cultivated plants. Second growth plants following fire or cutting have much better forms generally than others not so topped (Figs. 14, 15, 16). Old unpruned shrubs are commonly littered with dead branches and lopsided with bushy growth. Plants at

the Boyce Thompson Southwestern Arboretum have been kept pruned to hedge form for many years without deleterious effects. As a cultivated form, the single-stemmed bush with an open clear base is most desirable. Until desirable genetic forms are available, pruning will be necessary to control low lateral bushing, which interferes with harvest, and to shape the plant form suitable to all field operations. For economy of operation, machinery will have to perform the bulk of such work. No pruning techniques have been developed but some may be suggested for trial. Young bushy growth, for instance, may be cut by running over the plants with a disk, leaving only a few shoots aligned with the row. If done with a border disk this operation would also maintain the pyramidal border thus assisting in shunting the falling seed away from the plant stems.

The Huntington Botanical Garden experience of heavy pruning in conjunction with heavy yield indicates that pruning may be desirable to increase yield. Properly timed cutting possibly could concentrate yield and harvest to every other year with considerable harvest economy. This would appear to occur if foliage were also to be harvested as in a mowing operation. Seed can be readily separated from leaf and hulls by fan and screen, but handling the material at the proper drying stage may prove difficult without seed loss. Many problems would eventuate in such operations and will require the good minds and arts of the agricultural scientists engaged.

The Harvest. The seed as a farm product has been estimated to have a present day value of about 11 cents per pound as a sperm oil replacement and about 25 cents per pound as a hard wax (5). Even the higher figure of 25 cents per pound would eliminate jojoba as a crop if it is to be hand picked. Cost of hand picking seed in 100 pound lots for research purposes during 1957 was 40 cents per pound in Arizona and 25 to 33 cents per pound in Mexico. Although cultivated jojoba would provide improved conditions for hand picking, it is doubtful whether it could be done for less than 15 cents per pound and this would be excessive. Machine harvest is therefore regarded as prerequisite to economic harvest. Various methods have been suggested.

One is the shake-down machine recently developed for harvesting castorbeans (12). Other machines have been devised for stripping or shaking off bush berry crops (2). As seed fall is lingering and by degrees in jojoba, such methods would require repeated pasasges over the bushes and might be damaging. Several machines that gather nuts off the ground by sweep and suction are operating successfully in California (1). The ground is smoothed and rolled before the pick-up operation. Such new tools have already greatly advanced the prospects of engineering a comparable labor saver for jojoba. The large free-falling seeds enhance the outlook for jojoba. Field-cleaned seed could be delivered from the harvester to the waiting truck for a few cents per pound. Such a machine appears more immediately practicable than to await any genetically selected variety devised for hand picking, as the racemose cluster.

Conclusions

Jojoba has not yet had a fair trial as a cultivate. The Coit planting at Vista is the first to use progeny from cultivated stock. The several first attempts to cultivate at Harlingen, Texas, at Tucson and Florence in Arizona, and at Riverside and Murrieta in California show more failures than the successes at Vista and Huntington Botanical Gardens. However, the failures are due

more to lack of knowledge and attention to the plant than to its own natural limitations. The planters generally have not realized the sensitivity of the seedling, the slowness of healthy growth, its soil requirements, the delicate balance with water, and the great difference in genetic endowment between individuals and populations. The nature of the plant does not lend itself to the easily discouraged enthusiasm that naïvely seeks fortune on a chemical promise with wax as a password to a farming utopia. To be a successful cultivated crop, jojoba needs more than a profit motive for guidance. It needs the solicitous skill of an intelligent hand, learning as it works, to lead through the first several generations of plants. These first trials with jojoba are of great value to the serious student, the demonstrated failures especially so.

There are several first-steps necessary for the domestication of jojoba and they all need doing at once. We have taken stock of its weaknesses and have indicated its strength. The inherent variability of the plant is perhaps its greatest asset. Which of the several hundred genetic constitutions are best fitted for development and exploitation can only be determined by trials in several geographic environments. As first, second, and more generations are tested by plantings, the great majority of individuals can be expected to fail for lack of proper characters. The few that fit the requirements can then be improved by further selections, while the first best can provide stocks for the special agronomic problems involved. If we are fortunate in having a very broadly representative genetic base from which to select, the successful first selections should be obtained more rapidly than if we started with incomplete genetic stocks. Thorough field work, though costly in the beginning, would prove an economy in the long run. The erratic fruiting of jojoba under natural conditions increases the cost and difficulty of initial selection.

Jojoba appears to offer good genetic promise for a cultivated stock capable of yielding many times the wild production of seed, as agronomists learn how to culture and feed the potential. Considering the many amenities that could fall to man by the cultivation of jojoba, it appears that government or any other institution dedicated to posterity could find a very rewarding protégé in jojoba. However, because of its reluctant dragon character, it should be entertained as a tree crop. It is the kind of thing, which if successful, a man could plant for his sons. Its present prospects fully justify it as a research project, for the economic prospect is large. Few indeed are the native American plants which we can lay claim to making into cultivates. Jojoba may well try our prowess but as agricultural researchers we should not ignore it. Teleologically, we can say that jojoba is asking for it.

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Industrial Raw Materials of Plant Origin. IV. A Survey of *Simmondsia chinensis* (Jojoba)[1]

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I. Introduction

Simmondsia chinensis. This desert shrub of southwestern United States and Mexico, commonly known as jojoba or *Simmondsia*, is potentially a very valuable plant. Its value as a browse species in the desert regions has long been recognized, but only in fairly recent years has the vast application of the products of this plant been indicated. Most of these uses, which are as yet unexploited, originate from the liquid wax that comprises about fifty percent of the dark brown seeds.

II. History

The plant is known in botanical literature as *Simmondsia chinensis* (Link) Schneider of the family Buxaceae, as well as *Simmondsia californica* Nuttall (45, 46, 49, 53). The first of these names, being based on the first specific name that was given to the plant, is the correct one botanically although it perpetuates an error of geography. It is also known by various vernacular names including bucknut, bushnut, coffee berry, coffee bush, goat-berry, goat-nut, hohowi (the original Indian name), jojoba, jojobe, jojove, nutbush, pignut, quinine nut, sheepnut, and wild hazelnut (3, 8, 9, 19, 22, 25, 33, 39, 51, 55, 62). The first mention of the shrub in literature was by the Mexican historian Francisco J. Clavijero, who found that Indians of Baja California highly prized the fruit of jojoba for food and the oil as a medicine for cancer and kidney disorders (21). The Indians in Mexico also prize the oil as a hair restorer (23, 62).

Link (41) first described this plant, which he thought had been collected in China, in 1822 as *Buxus chinensis*. He failed to report it as being dioecious, as have numerous authors since (30). The name *Simmondsia californica* was assigned to the plant by Thomas Nuttall who collected specimens near San Diego, California. "*Simmondsia*" was chosen "In memory of Thomas William Simmonds, an ardent botanist and naturalist," "*californica*" denoting the type of locality (49, 62).

III. Characteristics

Simmondsia Oil. Simmondsia is unique among plants in that its seed contains an oil which is a liquid wax (for convenience hereafter referred to as oil) rather than a fat. (Waxes are esters of long-chain fatty acids with long-chain monohydroxyl alcohols, whereas fats are esters of long-chain fatty acids with glycerine.) The oil content of the seed does not decrease upon storing over a period of several years, and the properties of the oil are not altered. The oil of *Simmondsia* seed can be obtained by conventional means (i.e., expression and/or solvent extraction) and is a light yellow unsaturated liquid of unusual sta-

[1] Reprinted by permission of the authors and the Engineering Experiment Station, Georgia Institute of Technology. This article was selected to accompany the foregoing article in order to give as complete information as possible on jojoba. Only portions of this article have been selected for reprinting, and for full details, Bulletin 17 (Vol. 15(13): iii+1-36. 1953) of the Engineering Experiment Station should be consulted.—Ed.

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bility. The oil is obtained in a remarkably pure state and requires little or no refining for use as a transformer oil, a lubricant for high-speed machinery or machinery operating at high temperature, or for further processing to obtain the various other potential products (4, 6, 40, 43, 58). The residual meal from expression or extraction of the oil contains 30–35% protein and is quite acceptable as a livestock feed material. Its use in plastics has also been advanced (9, 26, 40). *Simmondsia* oil does not become rancid; it is not damaged by repeated heating to temperatures of above 285° C. or by heating to 370° C. for four days. The color is dispelled by heating for a short time at 285° C.; the oil does not change in viscosity appreciably at high temperature and requires little refining to obtain maximum purity (3, 4, 6, 9, 23, 40, 43, 46, 64). Since the material resembles sperm whale oil both in composition and in properties, it should serve well as a replacement for the applications of this oil (7, 8, 14, 15, 23, 34, 46, 61).

Simmondsia oil can be hydrogenated easily to a hard white wax (hereafter referred to as hydrogenated wax, solid wax, or wax) that has a melting point of about 73–74° C. and is second in hardness only to carnauba (27, 40, 45). It has been suggested that this wax may be made as hard as carnauba, and it should serve well in wax formulations to replace various imported waxes (10, 27, 45). In addition, the oil of *Simmondsia* is a potential source of both saturated and unsaturated long-chain fatty acids or alcohols (45, 46, 57, 58). The oil is also suitable for sulfurization to produce lubricating oil and a rubber-like material (factice) suitable for use in printing ink and linoleum (28, 29, 66, 67).

In 1910 a report was made on some pharmaceutical experiments and a preliminary analysis of the seeds of *Simmondsia*, but actually it did not establish the composition of the oil (50). Later Greene and Foster (33), at the University of Arizona, became interested in the oil because of numerous references

TABLE I

PHYSICAL AND CHEMICAL PROPERTIES OF *Simmondsia*-SEED LIQUID WAX *

Item	Amount
Glycerol	None
Oleic acid	0.66%
Palmitoleic acid	0.24%
Saturated acids	1.54%, 1.64%
Eicosenoic acid (C_{20}) **	30.3%
Docosenoic acid (C_{22}) **	14.2%
Eicosenol (C_{20}) **	14.6%
Docosenol (C_{22}) **	33.7%
Melting point	11.2°–11.8° C.
Solidifying point	6.7° C.
Flash point (C.O.C.)	555° F.
Fire point (C.O.C.)	640° F.
Viscosity S.U. at 100° F., sec.	127
Viscosity S.U. at 210° F., sec.	48
Viscosity index (Dean and Davis)	173
Color number (A.S.T.M.)	2
Corrosion at 212° F., copper strip	Nil
Pour point	10° C.
Carbon residue	0.01%
Refractive index at 25° C.	1.4648, 1.4650
Density at 25° C.	0.8642, 0.8990
Specific gravity 25°/25° C.	0.8635, 0.8640
Saponification number	92.2, 95.0, 165.7
Acid number	0.23, 0.32, 0.57
Iodine number (Hanus)	81.7, 88.4
Acetyl number	6.8
Reichert Meissl number	0.70
Polenske number	0.31
Unsaponifiable matter	37.62%, 48.3%
Iodine number of unsaponifiables	77.2, 79.3–80.2
Acetyl number of unsaponifiables	171.8, 172
Soluble acids (as butyric)	2.43%
Insoluble acids	59.43%
Iodine number of total fatty acids	76.1
Acid number of total fatty acids	172.0

* References cited: 32, 33, 35, 38, 44, 46, 64.

** The chief acid, eicosenoic, is reported to have the double bond between the 11 and 12 carbon atoms; the chief alcohol, docosenol, is unsaturated in the 13,14 position. The other alcohol, eicosenol, is probably unsaturated in the 11,12 position. The position of the double bond in the docosenoic acid was not established, but it has been suggested that it is erucic acid (unsaturated in the 13,14 position).

to its medicinal and culinary uses. Their work was the first to disclose the fact that the fatty matter of *Simmondsia* seed was a liquid wax, and they suggested that, because of this, it might have some value for lubricating purposes. Further investigation was then undertaken on the analysis of the oil. The results of determinations of the composition made in England by Green, Hilditch, and Stainsby (32) and in this country by McKinney and Jamieson (44) were published about the same time.

Table I summarizes the reported physical and chemical properties of the oil of *Simmondsia* seed.

Simmondsia oil is soluble in common organic solvents such as benzene, petroleum ether, chloroform, carbon tetrachloride, and carbon disulfide but is immiscible with alcohol and acetone.

In spite of the unsaturated nature of the oil it is not easily oxidized and does not become rancid even after standing for long periods of time. However, under proper conditions the oil may be made to react with sulfur to yield a stable product containing a relatively large amount of sulfur, which serves well as a lubricant or as an additive to lubricants. An improved high-pressure gear grease containing sulfurized *Simmondsia* oil sustained the highest pressure recordable on the S.A.E. (Society of Automotive Engineers) pressure lubricant testing machine (16, 29, 66).

Simmondsia oil has several advantages over the similar product from the sperm whale:

1. It possesses no fishy odor; *Simmondsia* oil has a mild, pleasant odor.

2. The crude oil contains no stearins and very little besides the liquid wax, so requires little or no treatment to prepare it for most industrial purposes.

3. It is native to North America and is a vegetable product, and as such, supplies would not be subject to the vagaries of nature to the extent that sperm whale oil is.

With reference to the sulfurized product:

4. *Simmondsia* oil will take up much larger amounts of sulfur than will sperm whale oil or lard oils (about 25% more).

5. *Simmondsia* oil does not darken to the same extent as other oils on sulfurization.

6. Highly sulfurized *Simondsia* remains liquid, whereas sperm oil, when highly sulfurized, requires mineral oil in order to keep it a liquid (66).

Other Products. By altering the conditions of the addition of sulfur to *Simmondsia* oil, a so-called factice may be obtained. This rubber-like material is suitable for linoleum manufacture and printing ink composition and has been suggested as a valuable material for the paint and varnish industries and the chewing gum industry (28, 46, 67).

The liquid oil is transformed into a hard white crystalline wax upon the addition of hydrogen, using nickel-copper catalyst and relatively mild temperatures and pressures. This solid wax has been shown to serve well in polishing wax formulations. A furniture wax polish composition of hydrogenated *Simmondsia* wax proved to be equal to or superior to some of the popular polishes now on the market. The same results were obtained with an automobile wax composed of hydrogenated *Simmondsia* wax. Insufficient experimentation has been conducted to establish the potentialities of this product from *Simmondsia*. It should be applicable in the many fields that require hard waxes. Since this wax is of high purity, it has been suggested that it would be advantageous to utilize other waxes as extenders in its compositions (2, 31, 40, 45, 46, 56, 58).

The desirability of further investigation of this wax, which could be produced in desert sections of the United States, is apparent in view of the fact that this

country is dependent upon foreign sources for all major vegetable waxes of commerce. Furthermore, no known wax source yields, or promises to yield, an amount of wax comparable to the large quantities that could be obtained from *Simmondsia*.

In addition to these products, *Simmondsia* offers a source of numerous other materials. Among these are the two long-chain monoethylenic normal alcohols and acids and the corresponding saturated alcohols and acids. These compounds are not readily available at the present time (common fatty acids contain 16–18 carbons and other common waxes do not contain large amounts of C_{20} and C_{22} straight-chain alcohols), and so their uses have not been extensively investigated. However, the uses of the alcohols in cosmetic preparations, in food preparation (as emulsifying agents), as detergents or wetting agents (as sulfonated material), and lubricants have been considered and show promise of great value. The alcohols have also been proposed as possible competitors of cetyl alcohol in petroleum products, as well as in the previously mentioned uses. There are various patents issued to cover uses of the alcohols derived from *Simmondsia* oil that attest to their potential value (27, 40, 43, 57).

The long-chain acids might have value in the preparation of soaps, although in all probability they would not prove to be as valuable as the other products. Apparently there is no reference in the literature to conversion of the wax acids of *Simmondsia* seed to the alcohols, but it should be possible, by adjusting the conditions of hydrogenation, to convert the oil (including the acid components) to the alcohols. In this manner the entire oil could be utilized for the preparation of alcohols if the acid portions were found to be of little value.

A considerable number of other unique chemical products is apparently available through reactions that are possible because of the chemical nature of the wax, alcohols, and acids that are available from the seed of *Simmondsia*. The development of these products will have to await the production of *Simmondsia* oil in large enough volumes to insure an adequate supply and to make feasible their investigation by industry.

The digestive systems of animals are not constructed to make use of waxy materials, and so the oil of *Simmondsia* is not suitable as a food. However, it has been suggested for use as a dressing for those people who enjoy rich salads but who wish to avoid calories. It reportedly has a pleasant taste, but if taken in more than small amounts it will have the same effect as mineral oil (46). This quality makes the oil a suitable carrier for medicinal preparations that must pass through the stomach into the small intestines before assimilation. It has also been found that *Simmondsia* liquid wax is useful in the stabilization of penicillin products. In fact, it has been shown to be the best liquid wax for this purpose. These preparations of penicillin are also suitable for hypodermic injection (36, 40, 46).

Simmondsia oil has been shown to inhibit the hydrolysis of vitamin A ester (65) and to have an intense inhibitory action on the growth of tubercle bacilli. "The virulent *Mycobacterium tuberculosus* when put in contact with the oil did not grow in the usual culture medium" (1). In connection with this latter fact, N. T. Mirov has suggested that *Simmondsia* should be valuable in studying the penetration of bactericidal agents through the waxy sheaths of tuberculosis bacilli. The liquid wax stored in *Simmondsia* seed is utilized during germination as fats are in other plant seeds; hence, Mirov feels that the seeds must contain an enzyme capable of hydrolyz-

ing waxes as lipase does plant seed fats. This enzyme may be capable of destroying the wax coating of tuberculosis bacilli (1, 45, 46).

IV. Economic Potential of *Simmondsia*

Markets for Simmondsia Products. There seems little doubt that markets for the products could be developed if the material were available in suitable quantity at a reasonable price, since it has been estimated by representatives of industry that 45,000 tons per year of *Simmondsia* oil could be used in this country. This estimate includes all uses where the oil and derivatives of the oil would be used as replacements for established materials and, also, other new uses which industrial organizations believe would be developed once the oil was made available.

The price received for the oil would depend upon the price its various products could command. Sufficient information for a detailed cost analysis on each of the uses of the oil is not available. However, several estimates have been made which present some basis for judgment. These estimates should be considered preliminary, however, since many of the potential users contacted have been unfamiliar with the material.

One of the uses of the oil is as a direct replacement for sperm whale oil. In the past 20 years the volume of sperm oil brought into this country has ranged from about 2 million pounds in 1932 to about 43.5 million pounds in 1951; these volumes are the totals of imports for consumption and United States and Alaska production. During the war years (1941–45) the supply of sperm oil was cut off almost entirely, since whaling expeditions to obtain the material were not feasible. This factor and the fluctuating price and supply history of sperm oil have led to interest by industry in a domestic source of a replacement. This interest is evidenced in the estimate made by representatives of industrial organizations that *Simmondsia* oil could replace sperm oil up to 100% in this country. This, of course, is based on a price for the oil competitive with that of sperm oil.

The potential for *Simmondsia* is increased by the possible demand for the hydrogenated wax. The various uses for this material, including its probable position as a replacement for carnauba wax, indicate relatively large volume potentialities . . . . The extent to which the wax can replace the volume of carnauba and other waxes used is questionable at this time, but preliminary estimates have been made. It has been estimated that, if the hydrogenated wax will replace carnauba wax, a market of 10 million pounds per year at half the price of carnauba is feasible. Conversely, if the wax will serve only as an extender for carnauba, the potential volume has been estimated at 20% of the yearly carnauba volume at about half the carnauba price. Samples of the hydrogenated wax have not been readily available. The interest of the wax industry in this hard wax, however, is apparent since numerous requests for samples have been received. Samples of the material should be made available, and after distribution to industrial organizations for evaluation much better estimates should be available as to the volume potential of the hydrogenated wax.

The estimated price at which the hydrogenated wax would have to sell, one-half the price of carnauba, would make it competitive with candelilla and carnauba. It has also been suggested that this wax might be competitive with ouricuri for some uses. These price and volume considerations indicate a substantial market for the hydrogenated wax of *Simmondsia*. Another factor of interest is that, in general, domestically produced

wax would be in a better competitive position than imported waxes, since such a material would not be subject to as great a fluctuation in supply and price.

Estimates as to the volume of *Simmondsia* oil that might be required for producing C_{20} and C_{22} alcohols and acids are not available since these materials are not produced in commercial quantities at present. However, an indication of price might be obtained by comparison with that of cetyl alcohol for which these materials have been suggested as supplements. Cetyl alcohol has sold for a number of years for about $1.50 per pound. The economic feasibility of producing the alcohols from *Simmondsia* oil has not been established. Consequently, investigation as to the utilization of the C_{20} and C_{22} materials is needed, as well as an economic evaluation of the processes by which these materials are obtained from the oil. These investigations and evaluations by industrial organizations, of course, are contingent upon having experimental quantities of the oil readily available.

The expanding demand, in recent years, for detergents and wetting agents indicates a need for stable supply sources of the starting raw materials used. At present, a relatively large volume of detergents is processed from imported raw materials. The extent to which *Simmondsia* oil could be used for this purpose would depend, of course, on the economics involved. However, if one considers the volume of detergents and wetting agents which is derived from materials that are similar to the components of *Simmondsia* (about 100 million pounds from sulfonated alcohols and 44 million pounds from sulfonated waxes, fats, and acids) (47), it can be said that this is another field in which there are vast potentialities which are definitely worthy of investigation.

The potential for *Simmondsia* oil for use in producing a factice is probably not a major one, but it would probably follow if the oil were available on the market.

One byproduct of value from *Simmondsia* seed, which should be of particular interest to the livestock producers in the areas where the plant is known to thrive, is the residual meal. The meal would be obtained after the oil had been extracted from the seed. It is comparable in protein value to linseed meal, and as a livestock feed supplement should find a ready market at about the price of linseed meal. Any estimates of actual volume demand for this material would be speculations; but based on the history of other oilseed developments, it seems likely that the material would be in demand at a price based on the protein content and on freight rates from the processing points for competitive meals.

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SUPPLEMENTARY NOTES ON JOJOBA UTILIZATION

Dr. W. H. Hodge has kindly given permission to publish as supplementary notes material which he had in his files on the properties and possible utilization of jojoba oil. At his request the U.S.D.A. Southern Utilization Research Branch made extracts of the jojoba seed (Fig. 1 & 2), and several analyses indicated that there are several interesting possibilities based on the principal components of the oil which are not mentioned in the foregoing article.

The oil is an excellent source for the chemicals listed below:

I.	$CH_3(CH_2)_7CH : CH(CH_2)_9COOH$	30.3%	Eicosenoic acid
II.	$CH_3(CH_2)_7CH : (CH_2)_{11}COOH$	14.2%	Docosenoic acid
III.	$CH_3(CH_2)_7CH : CH(CH_2)_9CH_2OH$	14.6%	Eicosenol
IV.	$CH_3(CH_2)_7CH : CH(CH_2)_{11}CH_2OH$	33.7%	Docosenol

Ozonolysis would give (at low cost) interesting long-chain aldehydo-alcohols and aldehydo-acids. Ozonolysis followed by oxidation would yield the following potentially valuable compounds (which are not available from commercial vegetable oils):

From I: A C_{11} dibasic acid (one more carbon than sebasic acid). Pelargonic acid.

From II: A C_{13} dibasic acid. Pelargonic acid.

From III: An omega-hydroxy C_{11} acid. A C_{11} dibasic acid (on further oxidation). Pelargonic acid.

From IV: An omega-hydroxy C_{13} acid. A C_{13} dibasic acid (on further oxidation). Pelargonic acid.

While pelargonic is a material of value, the hydroxy acids and the dibasic acids listed above should be of much greater value as intermediates for making synthetic lubricants, low-temperature plasticizers, tough fibers and plastics of the nylon type and heat-resistant rubbers.

Similar products could be made, of course, from the alcohols, III and IV. In addition, the C_{11} and C_{13} glycols

$$HO(CH_2)_{11}OH$$
$$HO(CH_2)_{13}OH$$

could be made readily. These have several obvious potentialities both in peace and in war.

Dibasic acids having an even number of carbon atoms, such as sebacic acid (10 carbons), are advantageous for some purposes, whereas the odd-carbon dibasic acids are preferable for other purposes. Both even- and odd-carbon dibasic acids could be made from *Simmondsia* oil. For example, ozonolysis of the eicosonic acid followed by reduc-

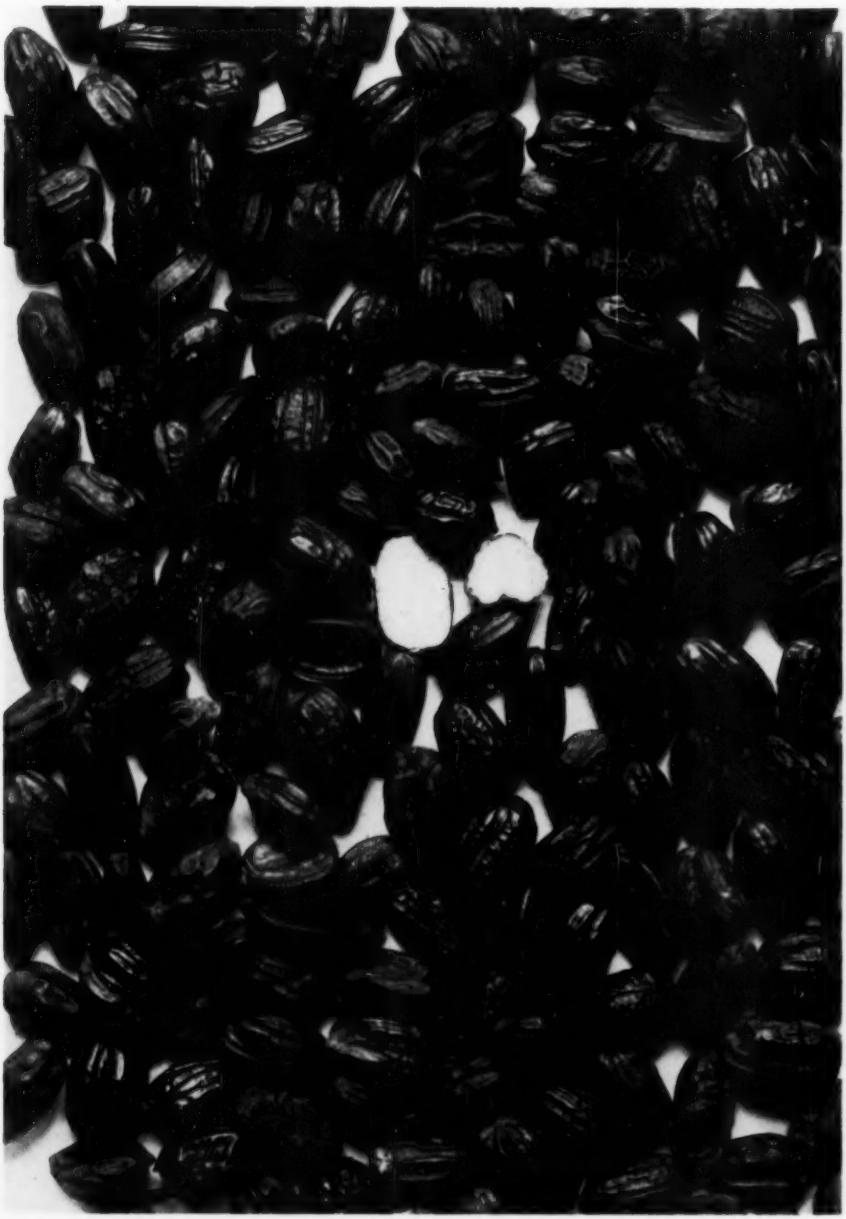

FIG. 1. Harvested seed of jojoba, *Simmondsia chinensis*, potential source of a valuable industrial oil. (Natural size.)

tion would yield omega-hydroxyundecanoic acid. Dehydration and oxidation of this acid would give sebacic acid:

$$HOCH_2CH_2(CH_2)_8COOH \rightarrow$$
$$CH_2 : CH(CH_2)_8COOH \rightarrow$$
$$HOOC(CH_2)_8COOH$$

Because these valuable products and many others that could be prepared from *Simmondsia* oil would not be competitive with those from conventional oils and fats, it seems possible that the *Simmondsia* plant is a potential new crop of great interest.

FIG. 2. The industrial products obtained from jojoba seed: at left (in vial) the yellow oil or "liquid wax" obtained from cold hydraulic press; at right the white hydrogenated wax. (Natural size.)

Isolation of Constituents of *Glottidium vesicarium*

The toxic plant, Glottidium vesicarium, *has been investigated for the presence of various constituents, and the isolation of three phytochemical constituents from the mature seeds has been described.*

N. O. NUESSLE[1] AND W. M. LAUTER[2]

The seeds of *Glottidium vesicarium* (Jacques) Harper have been shown to be toxic to farm animals (2, 4). Tests performed on the dried seeds by Foote and Gramling (5) indicated the presence of saponins and the absence of alkaloids. They succeeded in isolating two sapogenins in very small quantities. Inasmuch as this annual weed is widely distributed throughout Florida, it was decided to screen the plant and its seeds for various plant constituents and to utilize several different procedures (3, 7, 10) in order to obtain the sapogenins in larger quantities.

The annual weed often attains a height of 6 to 12 feet and has erect stems with several wide-spreading branches. The pods (usually containing two oblong seeds nearly 12 mm. long) are elliptical, pointed and bulged over each of the seeds. These pods remain on the branches long after all the leaves have fallen and may be responsible for the plant's common name, Bagpod.

The weed, while generally found growing along streams and drainage ditches in rich soil, is frequently found on higher land in fields which were formerly cultivated and in pastures. Its appearance during the spring and summer is similar to that of the cover crop, *Sesbania macrocarpa*, and as a result, it may grow undetected. Some ranchers, knowing that livestock will seldom eat it as long as they have ample forage, allow the plant to grow freely in pastures during the summer for the shade it offers to the grasses. It is usually in the winter, when severe weather reduces forage or when pastures are overgrazed, that cases of poisoning among cattle, sheep, hogs, goats, and even chickens have been reported (11).

Most farmers and ranchers in Florida do not consider the Bagpod to be dangerous since animals seldom eat it. However, if one animal in the group begins to eat the seeds, the others will also, even though the pasture contains ample forage. The death of 25 cattle in one herd during the fall of 1952 illustrates this occurrence. Experiments conducted as a result of these poisonings showed that one pound of the seeds was enough to kill a 672-pound steer (12). Thus, the Bagpod represents a great, potential hazard to all raisers of livestock in the coastal plain of southeastern United States.

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The authors wish to thank Dr. A. H. Gropp for interpretation of the infrared spectra and Professor Erdman West for his valuable aid in obtaining the plant material.

Experimental

Collection of Plant Material. The green immature plants, which were growing in semi-shaded, sandy loam, were

collected near Gainesville, Florida, in September, 1954. The materials were divided into three groups: roots, pods and seeds, and the remainder of the above-ground portion of the plant (henceforth called leaves and stems). Some of this material was used immediately for crude drug analysis, while the rest was stored at –15° until used.

The mature green seeds were also collected near Gainesville, Florida, in October, 1954, from plants growing in semi-shaded, sandy loam. The seeds were removed immediately from the pods and stored at –15° until extracted.

Crude Drug Analysis. Samples of the immature plants were immediately subjected to moisture determinations. Additional samples were dried in a circulating air oven for the other assays. The results of these analyses, which were performed as directed by the U.S.P. XV (6) and N.F. X (8), are shown in Table I.

Constituents of Immature Plant. The three groups of plant materials were coarsely ground and extracted with 95 percent ethanol in a modified Soxhlet extractor. Two hundred grams of each group of material were extracted and the extracts made up to the volume of 1 l. with 95 percent ethanol for saponin and flavanol testing. Aliquots of these solutions representing 5 grams were evaporated to dryness and the residues dissolved in 25-ml. portions of hot water and filtered through a sintered glass filter. These solutions were used for testing for the presence of alkaloids, tannins, organic acids and phenols. Chloroform solutions prepared in the same manner were used for tests for unsaturated sterols. The results of these tests are summarized in Table II.

TABLE I

CRUDE DRUG ANALYSIS

Determination	Percent found		
	Pods and seeds	Leaves and stems	Roots
Moisture	74.32	66.36	53.60
Total ash	4.47	3.09	14.70
Acid insoluble ash	0.09	0.12	10.89
Crude fiber	16.64	39.09	37.30
Ether soluble extractive:			
Volatile	1.03	0.82	1.27
Nonvolatile	1.72	2.11	1.05

TABLE II

PLANT CONSTITUENTS[a]

Constituent	Percent found		
	Pods and seeds	Leaves and stems	Roots
Flavonols	0.19	0.15	0.11
Tannins	0.07	0.25	0.00
Organic acids	0.10	0.10	0.08

[a] Calculated on a moisture free basis.

In addition to these tests, the extracts were examined for saponins by Wall's method (10), Bamford's procedure (1), with sulfuric acid, Fröhde's reagent, and sulfuric acid and ox bile. These tests gave results varying from negative to moderate. Only the root extract gave a positive test with sulfuric acid and ox bile.

The isolation of crude sapogenin acetate following Wall's procedure (9) and the isolation of saponin using barium hydroxide (7) were both unsuccessful.

Constituents of Mature Seeds. One kilogram of the mature seeds was coarsely ground and placed in 2 l. of hot 95 percent ethanol. After thirty minutes 375 ml. of water was added, and the mixture was allowed to macerate for two hours. After being agitated in a mechanical shaker for four hours and macerating overnight, the extract was removed by filtration and the mare extracted a second time. Both of these extracts gave positive tests with sulfuric acid and sulfuric acid and ox bile.

The two extracts were combined and concentrated at room temperature to 125 ml. As samples of this concentrate

showed appreciably diminished optical rotation upon acidification with HCl, a mixture of 5 volumes of HCl and 4 volumes of water was added to the concentrated extract. The precipitate which formed was removed after thirty minutes, dissolved in methanolic HCl, and refluxed for three hours. After the solution had cooled, it was made alkaline with NaOH, filtered, and thoroughly extracted with ether. Evaporation of the ether left a white solid which was washed with water and dried in vacuum. This yielded 15.6 mg. of Constituent I, melting with decomposition between 249° and 265°.

Additional precipitates were obtained from the acid mother liquor during a two-week period. These were combined and treated in the previously described manner, yielding 18 mg. of white material. Constituent II melted from 201.5° to 202.5° with decomposition.

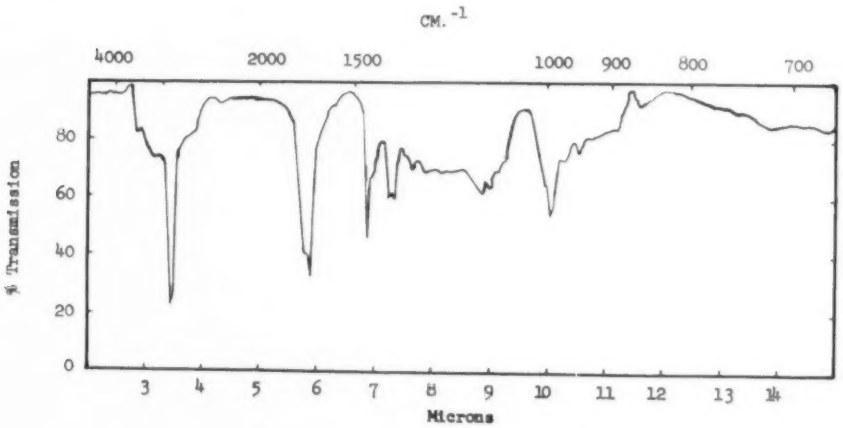
The semi-solid residue, which remained after the original combined extracts had been concentrated and filtered, was refluxed with a mixture of 200 ml. of methanol and 50 ml. of HCl. After the treatment described, it was washed with carbon tetrachloride and then with water. Upon drying, 14.8 mg. of Constituent III, decomposing at 241° to 242°, was obtained.

Infrared Spectra

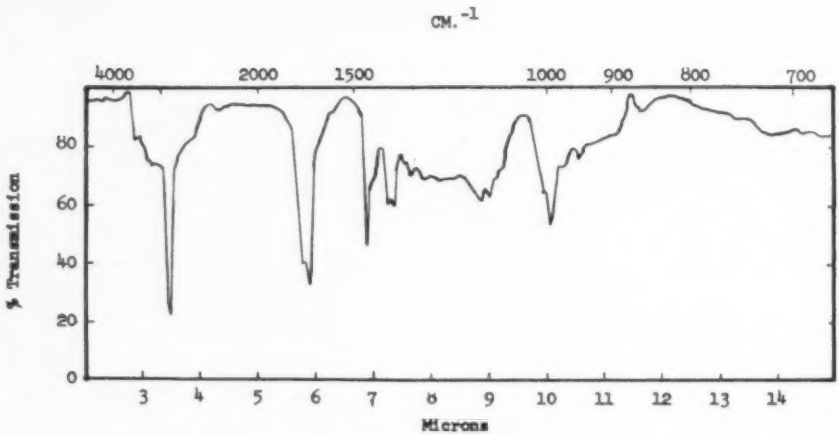
Infrared spectra of chloroform solutions of the three isolated products were obtained on a Perkin-Elmer Model 21 Infrared Spectrophotometer with a sodium chloride prism.

The absorption bands at 3,500 and 3,180 cm.$^{-1}$ show the presence of a hydroxyl group and the possibility of a nitrogen-hydrogen bond. The peak at 1,740 to 1,700 cm.$^{-1}$ is indicative of a carbonyl function, while the one at 1,000 cm.$^{-1}$ may be due to either a carbon-oxygen bond or a carbon-nitrogen bond. That the molecule is not a simple one, but rather that it is of a complex nature, is indicated by the absorption between 1,300 and 1,050 cm.$^{-1}$.

While the great similarity of the three spectra suggests the possibility that the three compounds are identical, slight variations are seen to exist in the carbon-hydrogen stretch band and the peaks at 1,105 and 1,130 cm.$^{-1}$. These variations,



INFRARED SPECTRUM OF CONSTITUENT I.



INFRARED SPECTRUM OF CONSTITUENT II.

as well as the differences in melting points, might be explained on the basis of isomerism or the presence of small amounts of impurities.

Summary

1. The results of crude drug analyses and screening tests for various plant constituents in different parts of the plant are reported, and attempts to isolate both saponins and sapogenins are discussed.

2. The isolation of three constituents from the mature seeds is described, and the infrared spectra of these products are discussed.

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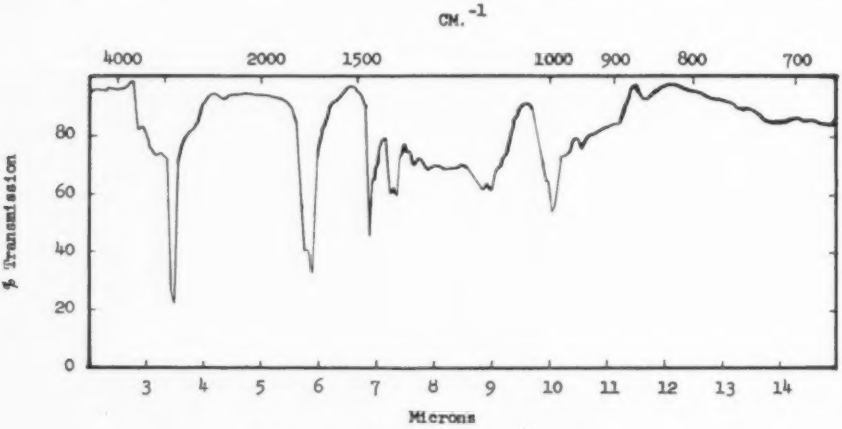

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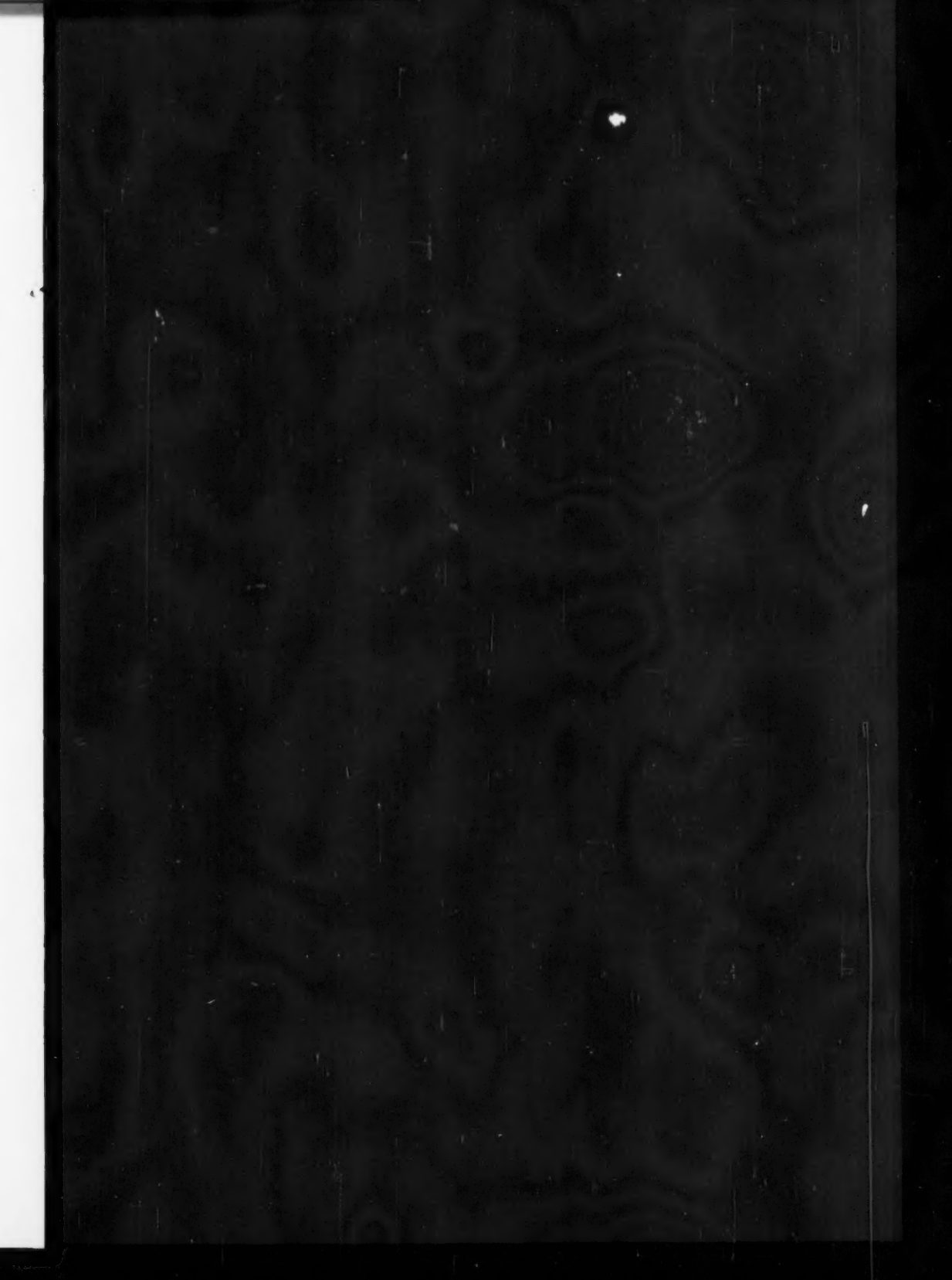
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